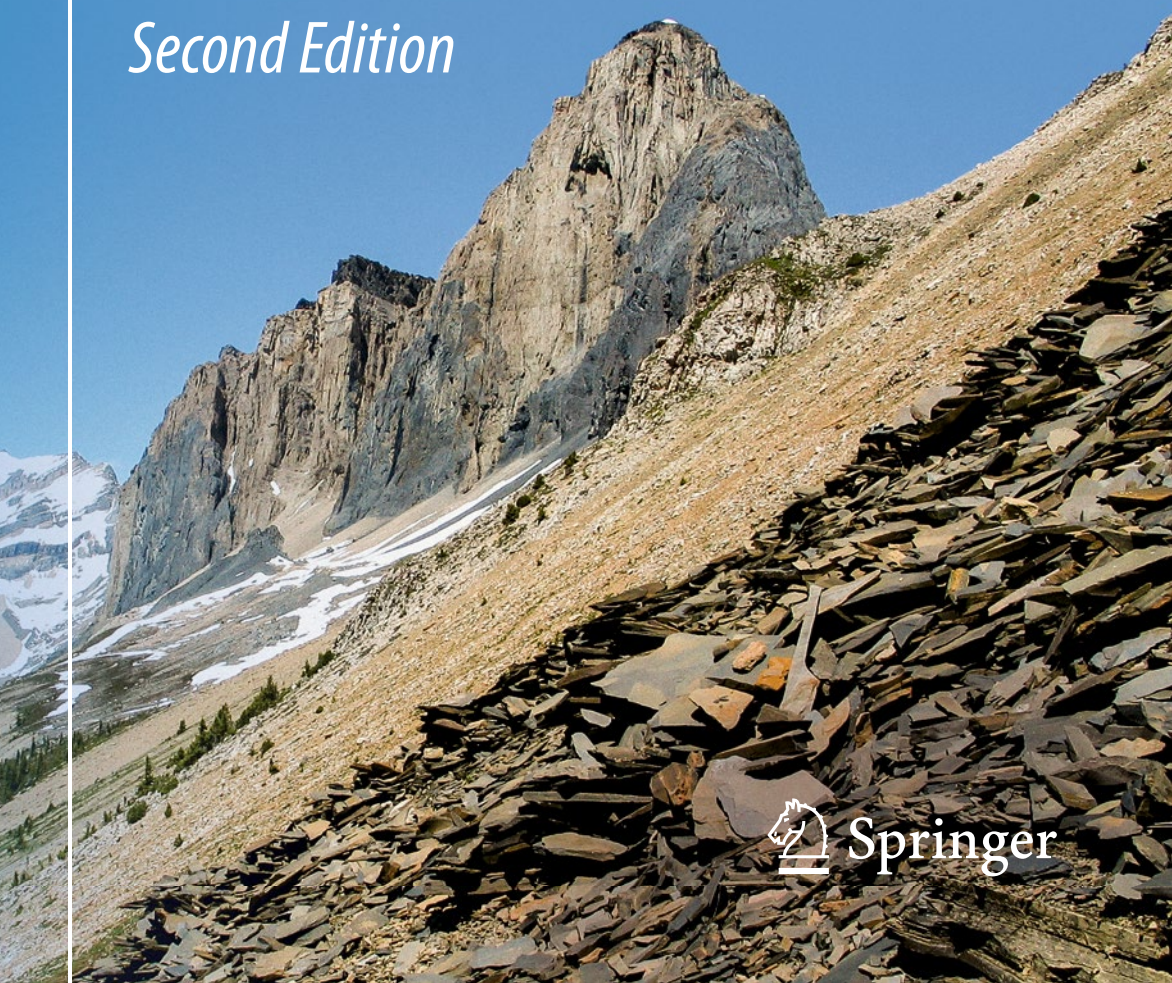
Robert L. Carlton

A Concise Dictionary of Paleontology

Second Edition



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Robert L. Carlton
Salem, OR, USA

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for Patricia

Introduction

A moderately comprehensive reference handbook covering the most important paleontological taxa, terms, concepts, and localities, this book is written primarily for general readers and beginning students in the field. My professional experience lies in technical writing and in teaching literature and history, with a lifelong interest in paleontology inspired by Professor Charles Higgins at UC Davis and by studying the geology collection in UC Berkeley's beautiful Bacon Hall before it was demolished in 1961. Using the essays of science writers like Loren Eiseley, Stephen Gould, and E.O. Wilson in my composition classes in the 1980s, I made critical thinking and the evolution of life on Earth the center of my teaching. An interesting technical writing project in the early 1990s showed me the lack of a dictionary like this, and I began the groundwork for a good reference work as I directed student research in the history of life in my writing courses. Retiring from teaching in 2014, I have widened my understanding of paleontology with intensive study in the last 5 years.

The lexicon of paleontology is of course too large to allow fully comprehensive coverage of taxa, concepts, or terminology in a small dictionary. My criteria for inclusion are necessarily flexible, as I attempt to cover the most significant taxonomic groups down to the level of orders, as well as the most significant genera and species in the literature. But in this second edition, in addition to covering these traditionally important taxa, I have increased my stress on certain categories. First, I focus on taxa associated with historical turning points such as mass extinctions and first appearances of derived characters; this approach of course emphasizes taxa that are the most important in biostratigraphy. Second, in addition to these transitional groups, I have included many entries that present phylogenetic problems because they do not fit neatly into established categories, thus inviting further research. Third, I bring together information from many sources on the most significant Konservat-Lagerstatten, which provide comprehensive information on the fossil communities and ecosystems of particular timeframes. Also, in the first edition, I often let one entry represent several taxonomic levels; I have now added many entries to cover more systematically the members of the groups that are paleontologically most important: trilobites, cnidarians, brachiopods, echinoderms

(especially crinoids and echinoids), mollusks (especially bivalves, gastropods, and cephalopods), ostracods, arthropods, early tetrapods, dinosaurs, pterosaurs, amphibians, therapsids, early mammaliaforms, and cetaceans and certain other mammals.

There are many science dictionaries, several of which purport to cover natural sciences or earth science, but I have found them all very unsatisfying for paleontology. Even the larger works like the *McGraw-Hill Dictionary of Scientific and Technical Terms* have minimal and often outdated coverage of the field, with very little detail on relationships and significance. And even in works with a focus closer to paleontology, such as the Allabys' *Oxford Dictionary of Geology and Earth Sciences*, there are still surprisingly few paleontological entries. So I believe there is a need for a more comprehensive dictionary covering paleontology alone. I have tried to maintain a mid-level tone, keeping the language accessible but including enough technical specificity to be useful for the serious student.

Online reference sites like the World Register of Marine Species, the Paleobiology Database, and Fossilworks are excellent for some basic information needed by specialists, but they are of little use to the general reader. Others like Palaeos.com and Prehistoric Wildlife provide readable and useful information and illustrations on many taxa. Wikipedia is the most valuable online reference, generally good in its detailed articles and up-to-date coverage, and I found some information in it for about three-fourths of my entries. Although it has surprising gaps and mistakes and sometimes reflects individual opinions that are not completely trustworthy, it provides more than enough information for general readers on the more familiar topics. *A Concise Dictionary of Paleontology* brings together the scattered information in these resources, supplementing it with the results of recent reading and research in many other sources.

It will be important for the reader to understand the structure of the entries and the procedures followed for terminology and dating, so let me explain. In the entries for taxa, I state the classification and other relationships first and then a physical description of notable traits. Measurements are generally in US terms, and length measurements are nose to tail unless otherwise specified. Wherever possible, I add further information, especially on the evolutionary significance of key organisms. The entries end with information on collecting localities and chronostratigraphic position. The references to geographic distribution indicate only the collecting localities of specimens, not necessarily the actual distribution unless so noted. The term "global distribution" excludes Antarctica, and the 40 listed taxa found in Antarctica are so identified. I use the term "cosmopolitan" for taxa with widely scattered and relatively sparse occurrences in appropriate environments.

All taxa listed as entries are extinct unless noted as extant. Most dates assigned to organisms and geological periods are approximate age ranges, but I indicate greater preciseness and certainty when possible. For dates and capitalization of the divisions of the time scale, I follow the Geologic Time Scale and the International Chronostratigraphic Chart (2018), as published by the International Commission on Stratigraphy. The latter provides the current names and dates of the most broadly accepted subdivisions of geological periods and epochs; here, I use the geochronological terms Era, Period, Epoch, and Age.

The entries for descriptive terms generally include only terms used in this dictionary, and they refer only to the paleontological application of the term. Geological and biological references are made only where necessary for their paleontological significance.

I have attempted to provide the most generally accepted taxonomic relationships, following the classifications given by the Paleobiology Database, and also its distribution information where it is given and not contradicted by other sources. But since paleontological description and taxonomy is by its nature a work in progress, with frequent changes in classifications as a result of ongoing work by specialists, there is no question of full coverage or even of up-to-the-minute accuracy. Newly described taxa increase every day both the range of first and last appearances and the range of geographic occurrences. So the names, classifications, locations, and dates given here are not to be taken as set-in-stone determinations but rather as signposts to provide access to further information about the taxa being discussed. With this in mind, I have tried to give at least two references to related taxa for each taxon entry. Of course, mistakes and omissions are inevitable in such an ambitious undertaking as this dictionary, and I will welcome all suggestions for improvement.

It has seemed advisable to steer a middle course between strict neo-Linnaean taxonomy and the extremes of modern cladistic systematics. As Colin Tudge so eloquently demonstrates in *The Variety of Life*, cladistic analysis is crucial in improving the accuracy of our picture of the tree of life. However, systematic taxonomy may blur the important distinctions between large groups such as dinosaurs and birds, or eurypterids and arachnids. At least for my purposes, when referring to reptiles in general, the paraphyletic classification Reptilia is far preferable to "non-avian, non-mammalian amniotes." Also, the idea that each node in the branching of the tree deserves a new rank is a leap too far, even for many professionals, and I have chosen to ignore subgroups like microclass, parvorder, and sub-tribe.

The Select Bibliography includes all of the important monographs that I have consulted, as well as many of the more important journal articles. But because writing a dictionary requires including information from several print and online sources for most entries, it is impracticable to fully document the sources. I would be very grateful for any corrections or other improvements in the dictionary or the bibliography; please send them to my son, Morgan Carlton, at ferric3.1@gmail.com.

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A

"*Aachenosaurus*" name given to a piece of petrified wood found in the Aachenian deposits near Moresnet, Belgium, and misidentified in 1888 as part of a duckbill dinosaur's jaw.

Aaptoryctes "unapproachable digger," a monospecific genus of insectivorous soricomorph mammals in the family Palaeoryctidae. From 4 to 5 inches long, the shrew-like *A. ivyi* probably had a stronger crushing dentition than its cousin *Palaeoryctes.* Wyoming, United States, late Paleocene, 57–56 Ma.

Aardonyx celestae a species of sauropodomorph dinosaurs in the clade Anchisauria. Known from disarticulated fragments of two individuals dated at 195 Ma, it is estimated to have been about 40 feet long. *Aardonyx* seems to be intermediate between the earlier prosauropods, which were generally smaller and often ran on their hind legs, and the later, more ponderous sauropods. Spion Kop, South Africa; Early Jurassic.

Abathochroal an unusual type of compound eye found only in the early trilobite families of the suborder Eodiscina, comprising a small number of lenses (about 70) with individual corneas.

Abavornis a proposed genus of primitive birds of the Late Cretaceous, about 85 Ma. Known only from a single bone in the shoulder process, it is tentatively classified as an enantiornithean. It was found in Uzbekistan in 1998 and given the species name *A. bonaparti*.

Abelisauridae a family of ceratosaurian theropod dinosaurs with two subfamilies, Majungasaurinae and Carnotaurinae. Known almost exclusively from Gondwana, they were perhaps the most successful large predators there in the Cretaceous. Bipedal, they are characterized by strong hindlimbs, almost vestigial forelimbs, and a variety of knobs and horns on a short skull. See also ***Arcovenator***, ***Carnotaurus***,

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Eoabelisaurus, ***Kryptops*, *Majungasaurus*,** and ***Rugops***. India, Africa, Madagascar, South America, and France; Middle Jurassic to Late Cretaceous, 170–66 Ma.

Abelisaurus a genus of theropod dinosaurs discovered in Patagonia. Known from a 35 inch incomplete skull, the type species *A. comahuensis* is estimated at 25–30 feet long and 16 tons. Argentina, Late Cretaceous, about 80 Ma.

Aberystwyth Grits a lower Silurian formation of deepwater flysch deposits consisting of alternating strata of shales and coarser sediments resulting from turbidity currents. Fossils are rare except for an extensive assemblage of ichnofossils, including several examples of Helminthoidea and *Palaeodictyon*. Wales, Early Silurian, 443–428 Ma.

Ablator a genus of spiders in the family Phrurolithidae; synonym *Abliguritor*. Almost an inch long, it is known only from Eocene amber specimens. Late Eocene, Europe and Russia.

Abliguritor see ***Ablator***.

Abrictosaurus a genus of basal ornithopod dinosaurs in the family Heterodontosauridae. The size of a large dog, about 5 feet long and nearly 100 pounds, it had a long tail and was bipedal and herbivorous. It had high-crowned teeth but lacked the canine-like teeth on the lower jaw that were typical of heterodontosaurids. Known from fragments of two individuals found in Lesotho, South Africa; Early Jurassic, 198 Ma.

Abrocomidae an extant family of caviomorph South American rodents in the suborder Hystricomorpha. Commonly known as rat chinchillas, the Abrocomidae diverged from the ctenomyids in the late Miocene, and two species can still be found in the central Andes. Argentina and Bolivia, late Miocene to Recent.

Abydosaurus a genus of herbivorous saurischian dinosaurs in the suborder Sauropodomorpha, discovered in 2010 at Dinosaur National Monument in Utah. Four skulls have been found, two of them entire, unusual for the relatively delicate head of a sauropod. Related to *Brachiosaurus*, *Abydosaurus* lived about 100 Ma. Its size is unclear because all four specimens are from juveniles about 25 feet long when they died; adult size is estimated between 30 and 45 feet long. United States, Early Cretaceous, 105 Ma.

Abyssal plain an extensive area of level ocean floor, near a continent but generally more than a mile deep.

Acantherpestes a genus of large spiny millipedes, archipolypod diplopods in the family Euphoberiidae. From 8 to 20 inches long, it had short, divided legs. Europe and North America, Middle Pennsylvanian.

Acanthoceras a genus of ammonitid ammonoids in the family Acanthoceratidae. Notable for a strongly ribbed shell with sharp knobs, it grew up to 2 feet high and a foot wide. *Acanthoceras* was widespread at the end of the Cenomanian and may have been able to hunt at great depths. Global distribution, early Cretaceous, 94–90 Ma.

Acanthochaetetes wellsi see **chaetetids.**

Acanthodes a genus of primitive acanthodiform fish in the family Acanthodidae. About a foot long, it had one dorsal fin and was edentulous, adapted to filter feeding. Global distribution; Early Devonian to Permian.

Acanthodii a paraphyletic and enigmatic class of primitive bony fishes in the infraphylum Gnathostomata, often called "spiny sharks." The first organisms to develop an efficient, moveable lower jaw, the acanthodians possessed characteristics of both chondrichthyans and osteichthyans. They are distinguished generally by a strongly heterocercal tail fin and several other stout spines supporting membranous fins, usually including two dorsal fins. The Acanthodii are now divided into three orders. The largest is the Climatiiformes, which includes two suborders of relatively small fish, the Climatiida and the Diplacanthida. The others are the nektic and predatory Ischnacanthiformes and the filter-feeding Acanthodiformes. Global distribution, late Silurian to late Carboniferous or early Permian.

Acanthostega a genus of stem-tetrapods intermediate between the lobe-finned fish of the Middle Devonian and the amphibians which began to colonize the land later in the period. The salamander-shaped *Acanthostega*, dated at 365 Ma, was 6 feet long and famously had eight digits on its forelimbs and seven on its hindlimbs. See **Tetrapoda**. Greenland, Late Devonian.

Acanthothiris an obscure genus of articulate brachiopods in the extant order Rhynchonellida and extinct family Acanthothiridídae. It is named for its numerous hollow spines. Europe, Asia, and Africa; Early to Late Jurassic.

Acanthothoraci "spine chest," an order of primitive placoderms, closely related to the rhenanids and also similar to the ptyctodonts except for having somewhat heavier armor. It bore a pair of strikingly large spines projecting from the chest. Global distribution, Early to Middle Devonian.

Acari an extant subclass of arthropods in the class Arachnida that includes the mites (Actinotrichida and Anactinotrichida) and the ticks (Ixodida). By far the most numerous group of arachnids, more than 30,000 species of mites are known, with a far greater number still undescribed. Global distribution, Early Devonian to Recent.

Acervularia a genus of cerioid rugose corals in the order Stauriida, suborder Columnariina, and family Acervulariidae. It constructed dome-shaped colonies

with tightly packed polygonal corallites. Europe and North America, middle Silurian to Middle Devonian.

Achaenodon a genus of pig-like artiodactyl mammals. Formerly called *Protelotherium*, it is variously placed in the Dichobunidae or the Helohyidae. It grew up to 7 feet long and probably weighed more than 600 pounds. North America and Africa, Eocene, 43–39 Ma.

Achelousaurus a monospecific genus of medium-sized centrosaurine ceratopsid dinosaurs, *A. horneri* is known from three skulls found in the Two Medicine Formation of Montana and Alberta. About 20 feet long and weighing about 3 tons, it is notable for a large skull and frill, with two small horns at the back of the frill. United States, Late Cretaceous, 74 Ma.

Achillobator a genus of large maniraptoran theropod dinosaurs in the family Dromaeosauridae. *Achillobator* was similar to *Deinonychus* but at least a third larger — the type species *A. giganticus* was very large for a dromaeosaur, up to 19 feet long. Mongolia, Middle to Late Cretaceous.

Achistrum a genus of sea cucumbers, holothuroids in the order Apodida and family Achistridae. Notable for very small hook-shaped spicules embedded in its skin, it was generally 3–4 inches long but sometimes grew as long as 2 feet. Known especially in nodules from the Mazon Creek assemblage, it is found in the United States, Carboniferous to Permian; Eurasia, Permian to Cretaceous.

Acidorhynchus see ***Saurorhynchus***.

Acipenseridae the sturgeons, a family of "living fossils," bony fish in the order Actinopterygii. Their ancestry reaches back to the Triassic, with true sturgeons appearing in the Late Cretaceous. They are notable for their size (the largest are more than 20 feet long and weigh more than a ton) and individual longevity (a century). Also notable for their longevity as a taxonomic family, being very little changed since the Cretaceous. Some species, such as the pallid sturgeon, *Scaphirhynchus albus*, are endangered because they are anadromous and often can no longer reach their spawning grounds. North America, Europe, and Asia; Triassic to Recent.

Acoelomate having no body cavity within which the animal's organs develop.

Acristavus a monospecific genus of hadrosaurid dinosaurs in the subfamily Saurolophinae. Known from two specimens from Montana and Utah, *A. gagslarsoni* is significant for its lack of skull ornamentation, sharply different from other saurolophines. United States, Late Cretaceous, 85–71 Ma.

Acritarchs "uncertain origin," not a taxonomic group but a large and varied group of organic-walled, non-carbonate, and non-siliceous organisms whose remains cannot be easily classified. Nevertheless, they are so abundant and diverse through the Precambrian and up to the Devonian that they are important as biostratigraphic markers, especially for times when other fossils are not abundant. At least some of the acritarchs are thought to be the resting cysts of phytoplanktonic algae, and they may be ancestral to the dinoflagellates. Dating back to 1400 Ma (even possibly more than 3000 Ma), the collection was grouped informally in form taxa in the 1990s on morphological criteria and wall structure, but it awaits classification on a more natural basis. The acritarchs seem to have declined markedly at the time of the Cryogenian Glaciation, about 650 Ma, and also during other periods of widespread glaciation. The Doushantuo Formation in Southern China contains an important collection of acritarchs, (such as ***Tianzhushania***, *q.v.)* from 590 to 565 Ma, during the Cryogenian Period.

Acrocanthosaurus a genus of North American theropod carnosaurs in the family Carcharodontosauridae. Named for its very high neural spines, it was large for a theropod, up to 38 feet long and 7 tons. United States, 120–110 Ma.

Acrodelphinidae a family of long-snouted cetacean mammals in the suborder Odontoceti; North America and Europe, early Miocene to early Pliocene.

Acrodonta an extant clade of lacertilian squamates in the suborder Iguania, including the Chamaeleonidae and Agamidae. Identified especially by an unusual dentition, the acrodonts appeared in the Early Jurassic and have spread worldwide except in the Americas (see ***Gueragama***).

Acrosalenia a genus of euechinoid sea urchins in the extant order Salenoida and family Acrosaleniidae. It is characterized especially by ridged teeth and stout, solid spines. Europe and Africa, Early Jurassic to Early Cretaceous.

Acrothele a genus of small inarticulate brachiopods in the order Lingulida and family Acrothelidae. Global distribution, middle Cambrian to Ordovician.

Acrotretida an order of inarticulate brachiopods in the class Lingulata; global distribution, early Cambrian to Recent.

Actiniaria the order of cnidarians called sea anemones. They are predatory, capturing floating prey with their numerous tentacles. Actiniarians are basically sessile, attaching to a hard substrate or burrowing in sediment. With no hard parts, they have a very sparse fossil record; the oldest known is ***Mackenzia***, *q.v.* See also **Ceriantharia**. Global distribution, Cambrian to Recent.

Actinistia a subclass of sarcopterygian fish that includes the living coelacanths and several extinct families of lobe-finned fish.

Actinocerida a subclass of middle Paleozoic nautiloid cephalopods. Generally straight, most were about 3 feet long, with a few somewhat larger. Found usually in shallow-water strata, they probably alternated between swimming and resting on the bottom, often preying from ambush. Global distribution, Early Ordovician to Carboniferous.

Actinocoelia a genus of lithistid sponges in the family Chiastoclonellidae. The silicified skeletons of *Actinocoelia* form prominent chert nodules in the Kaibab Limestone of the American Southwest. North America and China, middle to late Permian, 280–252 Ma.

Actinocrinites a genus of cameratan crinoids in the order Monobathrida and family Actinocrinitidae. Anchored to the substrate by a short stem, it was 4–5 inches long with a calyx up to only 1.5 inches wide. It lived worldwide in the Mississippian but may have existed from the Devonian to the Permian.

Actinocrinitidae a prolific family of cameratan crinoids in the order Monobathrida. They had a slightly domed base, and their surface differed from most crinoids in being composed entirely of calcitic plates. Global distribution, Devonian to Permian.

Actinopterygii "ray feather," the ray-finned fishes, a large class in the superclass Osteichthyes that includes most of the living bony fishes. The earliest actinopterygians appeared in the late Silurian (see ***Andreolepis***) and diversified rapidly in the Triassic. Fins consisting of thin, flexible skeletal rays supporting a membrane are the hallmark of the group. Global distribution, late Silurian to Recent.

Actinostromariidae a family of reef-building late Mesozoic demosponges, formerly considered stromatoporoids. Europe, Asia, and Mexico; Late Jurassic to Late Cretaceous.

Actinotrichida see **Acari**.

Adapidae a family of early primates in the suborder Strepsirrhini, probably diverging from the Plesiadapiformes in the late Paleocene, about the same time as the Omomyidae; the type genus is *Adapis*. They are generally considered to be related to the North American notharctids, including *Notharctus* and *Smilodectes*, and are possibly ancestral to the lemuroids. Europe, North America, and Asia; late Paleocene to late Miocene.

Adaptive radiation a sudden increase in diversity within a group of organisms, resulting from environmental changes that open new ecological niches in a geographically isolated area. The marsupials of Australia and Darwin's finches on the Galápagos Islands are the most widely known examples, and one of the most scrupulously described is E.O. Wilson's groundbreaking study in the 1950s of ant speciation on the island of New Caledonia.

Advanced of organisms – a state derived from a more primitive form, more modified and specialized than primitive ancestral species.

Aechminidae a palaeocopid family of ostracods in the suborder Beyrichicopina. The aechminids had lobate shells with a single dorsal spine. Global distribution, Ordovician to early Permian.

Aeduella a genus of chondrostean actinopterygian fish in the order Aeduelliformes. *Aeduella* was similar to the Early Carboniferous *Canobius*, especially in its vertical jaw suspension. North America and Europe, early Permian, 299–290 Ma.

Aeger a genus of shrimplike decapods in the family Aegeridae. Well-known from the Solnhofen quarry of Germany, *Aeger* was about 8 inches long, with a large, projecting beak. Europe, North America, and Asia; Triassic to Early Cretaceous.

Aegyptocetus a genus of semiaquatic archaeocete whales in the family Protocetidae. It is notable for cranial features that gave it the ability to hear underwater but also for spinal features similar to those of other terrestrial weight-bearing protocetids such as *Rodhocetus*. Egypt, middle Eocene.

Aegyptopithecus a genus of early anthropoid primates in the suborder Catarrhini, closely related to the smaller *Propliopithecus*. From 2 to 3 feet long, it was probably herbivorous and arboreal. Fayum, Egypt, late Eocene, 34 Ma.

Aegyptosaurus a genus of titanosaurian sauropod dinosaurs, about 50 feet long and weighing 12 tons. It had a long neck and tail and had relatively long legs for a sauropod. The only known specimens were discovered by Ernst Strömer but were lost during World War II. North Africa, Cretaceous, 106–94 Ma.

Aelurognathus "cat jaw," a genus of small therapsids in the family Gorgonopsidae and subfamily Rubidgeinae; also called *Prorubidgea*. Known from several specimens from the Karoo Basin, it was about 2 feet long and had very long canine teeth. South Africa, late Permian.

Aelurosaurus a genus of small carnivorous therapsids in the family Gorgonopsidae. Best known in the type species *A. felinus*, it was probably about 2 feet long. South Africa, late Permian, 259–254 Ma.

Aeluroidea a superfamily of carnivorous mammals in the suborder Feliformia. It includes the Felidae, Hyaenidae, Viverridae, and possibly Herpestidae (mongooses). Early Oligocene to Recent.

Aepycamelus a genus of giraffe-like artiodactyl mammals in the family Camelidae. About 10 feet tall, with long legs and a long neck, they browsed in open grassland. United States, early to late Miocene.

Aepyornis a genus of giant ratite birds in the order Aepyornithiformes and family Aepyornithidae. With the removal of *Aepyornis titan* to the genus *Vorombe*, two species of *Aepyornis* and the related *Mullerornis* comprise the Aepyornithidae, the group called elephant birds. They all became extinct after humans arrived in the Holocene. Madagascar, late Pleistocene to Recent.

Aerosteon riocoloradensis a species of carnivorous dinosaurs from 85 Ma, notable for breathing the same way as modern birds do, with a bellows-like pulmonary system; Argentina, Late Cretaceous.

Aethocrinus a genus of early crinoids, generally considered the earliest known. France, Early Ordovician, 488–478 Ma.

Aethophyllum an unranked monospecific genus of herbaceous conifers. Low-growing and spreading, *A. stipulare* differs from most fossil conifers, which were trees. Europe and China, Middle Triassic.

Aetiocetidae a family of basal-toothed mysticete whales, notable for representing one of the transitional steps between toothed and baleen whales. From 10 to 26 feet long, aetiocetes were toothed but also possessed nutrient foramina and therefore probably some form of baleen, a synapomorphy of baleen whales. See also **Mammalodontidae**. British Columbia, Washington, Oregon, Mexico, and Japan; early to late Oligocene.

Aetiocetus a genus of early mysticete whales in the family Aetiocetidae. An example of the transition between the early toothed whales and the modern baleen-bearing mysticetes, it was toothed and also probably had some baleen. Widespread in the North Pacific Ocean during the Oligocene, 30–20 Ma.

Aetodactylus halli a species of ornithocheirid pterodactyloid pterosaur from the Early Cretaceous. It had a wingspan of 9 feet and a long, narrow snout lined with sharp, fish-catching teeth. See also ***Cimoliopterus*****;** Texas, 97 Ma.

Aetosauria "eagle lizard," a monofamilial order of crocodilian archosaurs, consisting of the family Stagonolepididae. Generally well-armored, the aetosaurians ranged from 3 to 10 feet long. Several genera bore heavy, backward-projecting spines to protect the back, and some are important Triassic index fossils. Although known only from the Late Triassic, they probably originated in the Middle or even Early Triassic. Global distribution, Late Triassic.

Afairiguana avius a species of small squamates in the suborder Iguania and family Polychrotidae. A specimen found at Fossil Butte in Wyoming is the oldest complete specimen of an iguanian lizard from the Western Hemisphere. United States, early Eocene, 56–50 Ma.

Afrosoricida a proposed order of mammals to include the tenrecs (Tenrecidae) and golden moles (Chrysochloridae); Africa and Madagascar, Oligocene to Recent.

Afrotarsius a genus of haplorrhine primates in the family Tarsiidae, known from several fragments found in North Africa and Burma; Africa and Asia, Eocene to Oligocene.

Afrotheria a large clade that includes the clade Tethytheria (proboscideans, sirenians, and desmostylians) as well as other genera that evolved in Africa, such as the aardvarks, tenrecs, and hyraxes. See also **Eutheria**. Paleocene to Recent.

Afrovenator a monospecific genus of theropod dinosaurs in the family Megalosauridae, known from a single, relatively complete skeleton. Up to 27 feet long and similar to *Allosaurus*, *A. abakensis* was smaller than *Tyrannosaurus rex* but was an efficient predator with strong forelimbs and sickle claws. Niger, Middle Jurassic, 193 Ma.

Aganaster a genus of brittle stars, ophiuroids in the order Ophiurida and family Aganasteridae. About 1 inch wide, it had a distinctive flower-like central disc and short, slender arms. United States, Middle Mississippian, and China, late Permian.

Agate Fossil Beds National Monument a site of lower Miocene volcaniclastic deposits in northwestern Nebraska, notable for specimens of several mammal species that are slightly different from similar species of the Oligocene White River Group fauna of the same area. One of the most striking is the helical burrow of ***Palaeocastor***, *q.v.*, and others are *Amphicyon*, *Miohippus*, and the chalicothere *Moropus*. United States, early Miocene.

Agathoxylon a genus of large gymnosperm trees in the family Araucariaceae; Europe, South and North America, Africa, and Antarctica; Middle Jurassic to late Miocene.

Agilisaurus a monospecific genus of ornithischian dinosaurs, probably related to *Heterodontosaurus*. About 4 feet long and lightly built, *A. louderbacki* was optionally quadrupedal but agile and a fast runner bipedally. Known from a single complete skeleton dated between 168 and 161 Ma, it has the typical ornithischian beak-like predentary structure. China, Middle Jurassic.

Agilodocodon scansorius a species of Jurassic therapsids in the suborder Docodonta, found in the Tiaojishan Formation and dated at about 160 Ma. Described in 2015 as only 5–6 inches long, the shrewlike *Agilodocodon* is the earliest-known tree-climbing mammaliaform animal. It had spade-shaped teeth, long claws, and flexible elbows and ankles and probably fed on sap by gnawing through tree bark. Yanliao biota, China, Late Jurassic.

Aglaophyton a genus of pre-vascular plants in the superphylum Polysporangiomorpha. A land plant growing about a foot high, *Aglaophyton* is notable as a transitional plant between bryophytes and vascular plants. Known only from the Rhynie Chert, Scotland, Early Devonian, 410–405 Ma.

Aglaspidida an order of arthropods, generally considered to be related to the chelicerates but now placed in the class Artiopoda. They are superficially similar to a trilobite with the elongate tail spine of a horseshoe crab. North America, Europe, Asia, and Australia; early to late Cambrian.

Agmata a proposed short-lived phylum erected in 1977 to include the enigmatic fossils *Salterella* and *Volborthella* of the early Cambrian; reaffirmed in 2003 but still controversial.

Agnatha a superclass of jawless fish that includes several extinct groups (generally considered to be the Conodonta, Pteraspidomorphi, Cephalaspidomorphi, Myllokunmingiidae, and Haikouellidae) and the extant Cyclostomata. The agnathans include the long-extinct ostracoderms and conodonts as well as the modern lampreys and hagfish. See also **Gnathostomata**. Global distribution, early Cambrian to Recent, 535–0 Ma.

Agnosphitys a monospecific genus of early dinosaurs, placed variously in the families Guaibasauridae and Silesauridae. Dated about 206 Ma, *A. cromhallensis* is known only from partial remains but seems to be a stem-dinosaur. England, Late Triassic.

Agnostida a primitive order of small early trilobites. Isopygous and generally eyeless, they had only two or three thoracic segments. Some genera are thought to be planktic, but most are benthic like most other trilobites. Global distribution, early Cambrian to Late Ordovician.

Agnostotes orientalis a species of agnostid trilobites in the family Diplagnostidae. Isopygous and blind, it is the index fossil for the beginning of the Jiangshanian Age near the end of the Cambrian, 494 Ma. Cosmopolitan.

Agnostus a genus of small trilobites in the order Agnostida and family Agnostidae. About 0.2 inches long, like all agnostids, *Agnostus* was eyeless and isopygous. One of the earliest trilobites, it is especially prominent in Cambrian deposits. North America, Europe, and Asia; early Cambrian to Early Ordovician.

Agoniatitida an early order of primitive ammonoids, ancestral to all later ammonoids; synonym Anarcestida. Global distribution, Early to Middle Devonian.

Agorophius a poorly known genus of early odontocete whales in the family Agorophiidae; synonym *Zeuglodon pygmaeus*. First named by E.D. Cope in the

1870s, the family was long in question because the holotype of the genus was lost, but a 2016 description of a skull of *Agorophius pygmaeus* substantiates its position as a basal odontocete. South Carolina, United States, middle to late Oligocene, 28–24 Ma.

Agriochoeridae a family of artiodactyl mammals in the suborder Tylopoda and superfamily Oreodontoidea. Superficially pig-like or sheep-like and as large as a small horse, they are now generally thought to be related to camels. Less advanced than their cousins the Merycoidodontidae, they had a selenodont dentition and large claws instead of hooves, rare for artiodactyls. Widespread in North America but especially well-known from specimens in the Turtle Cove fauna of the John Day Fossil Beds. North America, late Eocene to early Miocene.

Agriotherium "hunting beast," a genus of early bears in the subfamily Agriotheriinae; formerly called *Hyaenarctos*. Mainly carnivorous and about 9 feet long, it was among the larger bears of the Pliocene. North America, Europe, Asia, and Africa; late Miocene to early Pleistocene.

Aigialosauridae a family of semiaquatic varanoid lizards in the order Squamata and extinct superfamily Mosasauroidea. The type genus is *Aigialosaurus* (formerly called *Opetiosaurus*). About 3 feet long, the aigialosaurs show some aquatic specializations — a slightly flattened tail and reduced limbs — but were not structurally different from terrestrial ancestors. Considered basal mosasaurs, they are important as the earliest-known ancestors of larger and more specialized mosasaurs, which appeared about 92 Ma. The monophyly of the family is in question. Europe, Late Jurassic to Late Cretaceous (Cenomanian).

Ailsacrinus a genus of crinoids in the order Millericrinida. Its calyx was 1–2 inches wide and rounded or conical. It had a short stem but seems to have been free-living, often found unattached with no stem. Known especially from a massed assemblage in the type locality in Gloucestershire. England, Middle Jurassic.

Aïstopoda an order of snakelike amphibians in the subclass Lepospondyli. Ranging from 2 inches to 3 feet in length, some had reduced limbs, but most were limbless. They appeared 20 million years after the first tetrapods. North America and Europe, Early Carboniferous to middle Permian.

Ajacicyathus a genus of early colonial or solitary archaeocyathan sponges; global distribution, early Cambrian.

Aktiogavialis a genus of gharials in the superfamily Gavialoidea and subfamily Gryposuchinae. Known from fragmentary remains found in Puerto Rico and Venezuela, Oligocene to Miocene.

Alamitophis tingamarra a species of snakes in the family Madtsoiidae. Found at the Murgon Fossil Site in Australia, it is related to two other species of the genus found in Argentina, one of many pieces of evidence about the migration of many species from South America to Australia when they were still connected by Antarctica. Australia, early Eocene.

Alamosaurus sanjuanensis "cottonwood lizard," a species of titanosaurian sauropod dinosaurs in the family Saltasauridae. Known from many fragmentary specimens and a nearly complete juvenile skeleton found in 2002, *Alamosaurus* was among the last surviving dinosaurs and possibly the largest North American dinosaur. Some estimates claim that it may have weighed 80 tons and been 100 feet long. It was first found in the Kirtland Formation of the San Juan Basin, New Mexico, and other specimens have been found in Utah and Texas. United States, Late Cretaceous, 70–66 Ma.

Albanerpetontidae a long-lived family of salamander-like lissamphibians in the extinct order Allocaudata. They were fossorial, with a robust head and neck; North America and Europe, Middle Jurassic to Pliocene.

Albertosaurus a genus of large tyrannosaurid theropod dinosaurs, 27 feet long and 2–3 tons in weight. *Albertosaurus* had two digits on a very small manus and a skull more than 3 feet long with about 60 teeth. The most significant find of *Albertosaurus* was made by Barnum Brown in 1910, in the Dry Island bone bed on the Red Deer River. Excavations there over the next century have uncovered more than 1100 bones from two dozen individuals, evidence of pack behavior or at least gregariousness. North America, Late Cretaceous, 70–66 Ma.

Albumares brunsae a species of trilobozoan Ediacaran fossils. It was round and flattened, with three oval arms radiating from the center and branching furrows covering the surface. Russia, late Ediacaran, 560–555 Ma.

Aleodon a genus of cynodont therapsids placed tentatively in the family Chiniquodontidae. Poorly known from several specimens, *Aleodon* was similar in size and in several key features to other Late Triassic cynodonts that are close to the line of descent leading to stem-mammals. See also ***Brasilitherium***. Tanzania, Namibia, and Brazil; Late Triassic, about 237 Ma.

Alethopteris a genus of large seed ferns in the family Medullosales. It had very long fronds, foliage in the form genus *Pecopteris*, and bark in the form genus *Knorria*. Global distribution, Early Carboniferous to Early Cretaceous.

Aletopelta coombsi a genus of armored dinosaurs in the family Ankylosauridae. Known only from a partial articulated skeleton found in Southern California, *A. coombsi* was about 16 feet long. It was named "wandering shield" because in the Late Cretaceous, the formation in which it was found was several hundred miles to

the south, off the coast of Mexico. The body was washed out to sea and briefly became a reef colonized by shellfish. United States, Late Cretaceous, 85–71 Ma.

Alienoptera a poorly known order of insects in the superorder Dictyoptera, known only from Burmese amber but seemingly foreign to other dictyopterans; Late Cretaceous, 100 Ma.

Allochthonous referring to a fossil assemblage consisting of organisms removed from their place of origin before burial, as opposed to an autochthonous assemblage buried in situ; see also **taphocoenosis**.

Allodesmus a genus of pinnipeds in the extinct family Desmatophocidae. More than 8 feet long and about 800 pounds but sexually dimorphic (females were smaller); all four feet were webbed. Six species are known, the most recent being *A. demerei*, described in 2018. *Allodesmus* had large eyes and was adapted to hearing underwater sounds. North Pacific Ocean: North America and Japan, Miocene.

Allonia a genus of chancelloriids, one of the earliest known. It had a near-global distribution, well-known from the Burgess Shale and the Guanshan biota and found also in Europe, Australia, and elsewhere in Asia; early to late Cambrian, 522–490 Ma.

Allorisma a genus of marine bivalves in the order Pholadomyida and family Edmondiidae. Up to 2.5 inches long, its shell is roughly oval, with a blunt beak and a posterior gape. Global distribution, Silurian to late Permian.

Allosauridae a family of theropod dinosaurs, traditionally considered saurischians. Ranging from 20 to 32 feet long, the allosaurs were bipedal predators, generally slightly smaller than *T. rex*. One of the later species, however, known only from a skull recently discovered in Wyoming, was at least as large. They had three fingers; their forelimbs were short but more robust than later large theropods; and the brain was primitive, with large olfactory bulbs. Known mainly from western North America but also found in Portugal and possibly in Tanzania; Late Jurassic, 155–146 Ma.

Allosauroidea a superfamily of theropod dinosaurs, generally considered to include the closely related Carcharodontosauridae and Neovenatoridae and also the Allosauridae and Metriacanthosauridae. Global distribution, 176–91 Ma.

Allosaurus fragilis the type species of the theropod genus and the family Allosauridae; United States and Portugal, 151–146 Ma.

Altirhinus a monospecific genus of iguanodont ornithischian dinosaurs. With a tall beak on a rounded snout, *A. kurzanovi* was 21–26 feet long. It was optionally quadrupedal and had five digits on the manus, including a thumb spike. Its arched snout

is similar to that of *Muttaburrasaurus*, and the two share several other similarities. Mongolia, Early Cretaceous, 125–100 Ma.

Altriciality of animals' young, born relatively undeveloped and needing parental care. See, for example, ***Maiasaura***, ***Rapetosaurus***, and **Teleostei**.

Alula the first digit on each wing in modern birds. A short projection on the leading edge with a small number of flight feathers, the alula improves the bird's maneuverability in flight. It first appears in the fossil record in primitive birds in the Early Cretaceous (e.g., *Eoalulavis* and possibly *Protopteryx*), but its evolutionary development is unclear.

Alum Shale Formation an upper Cambrian formation in Scandinavia; see **Orsten Lagerstätten**.

Alvarezsauroidea a superfamily of maniraptoran dinosaurs that includes the Alvarezsauridae and *Haplocheirus*. Most have been found in China and Mongolia in the Late Cretaceous, but the earliest and largest, *Haplocheirus sollers*, is dated at 160 Ma. Laurasia, Late Jurassic to Late Cretaceous, 160–66 Ma.

Alveolites a genus of colonial favositid corals in the subclass Tabulata. Diverse and widespread from the Silurian to the Devonian but declining after the Early Carboniferous, it had compressed, thin-walled corallites in massive or branching bodies. Global distribution, Silurian to Permian.

Alveugena a genus of nonplacental mammals in the family Cimolestidae, possibly ancestral to the taeniodonts; known only from two partial specimens. United States, Early Paleocene, 66–63 Ma.

Amaltheus a genus of ammonoids in the order Ammonitida and family Amaltheidae. Involute and up to 9 inches high, it had strong ribbing and a prominently braided keel. Occurring only between the strata of its relatives *Prodactylioceras* and *Dactylioceras*, it is an important index fossil in the Pliensbachian. Global distribution, Early Jurassic, 186–184 Ma.

Amargasaurus cazaui a species of sauropod dinosaurs in the family Dicraeosauridae. Known only from an almost complete skeleton discovered in 1984, *Amargasaurus* was about 40 feet long and 9 feet tall; its weight is estimated at 7,000 to 8,000 pounds. It is notable for an unusual double row of long vertebral spines from the base of the skull along the entire long neck. Argentina, Early Cretaceous, 130 Ma.

Amber fossilized tree resin, resulting in an unusual sedimentary deposit. Although they have the drawback of not being able to be handled, amber fossils of insects, arachnids, and plants preserve exceptional detail and help to fill out the relative

paucity of terrestrial deposits. Amber deposits are the principal source of spider fossils, and even though very few vertebrate fossils occur in amber, bird feathers and even a nestling enantiornithean bird in amber are known from about 100 Ma. Since amber occurs near trees, sometimes far from the more common aquatic depositional environments, it provides a unique sampling of the biota. The earliest amber fossils are known from the Triassic, occurring in small amounts globally. The Baltic amber of the Eocene has produced the greatest concentration of fossils, with important discoveries also in Cenozoic Dominican and Burmese amber deposits.

Ambiortus a controversial genus of primitive birds. Generally classified in the Ornithomorpha, it is poorly known, and its phylogenetic relationships are unclear. Early Cretaceous, about 130 Ma.

Amblypoda a discarded term for a polyphyletic grouping of extinct ungulates including the uintatheres and pantodonts.

Amblypygi "blunt rump," an order of chelicerate arthropods in the class Arachnida. Up to an inch long, they are known as whip spiders or tailless whip scorpions. With a flattened body and posture, they have long, slender legs and no silk spinnerets. They have no tail or venomous fangs, but their spiny pedipalps can puncture their prey. Dating back to the Pennsylvanian (*Graeophonus*), about 160 species are presently known in tropical and subtropical areas. Cosmopolitan, Late Carboniferous to Recent.

Ambondro mahabo a species of early mammals in the yinotherian family Henosferidae, probably close to the lineage of monotremes; Madagascar, Middle Jurassic, 167 Ma.

Ambonychia a genus of myalinid marine bivalves in the family Ambonychiidae; synonym *Byssonychia*. About 2 inches long, the shell has strong radial ribbing and a small, sharp beak at the hinge. Europe, North America, and Australia; Middle Ordovician to early Devonian.

Ambopteryx longibrachium see **Scansoriopterygidae**.

Amborella an extant genus of Early Cretaceous plants in the family Amborellaceae, considered a possible ancestor of angiosperms; global distribution, 130 Ma to Recent.

Ambulacrum plural ambulacra. In echinoderms, it is a radial zone (usually in a groove) of pores on the surface through which the tube feet protrude.

Ambulocetus a genus of archaeocete whales in the family Ambulocetidae. About 10 feet long and more than 600 pounds, it was named "walking whale" because it was an important transitional form between ancestral land-dwelling mammals and

fully marine mammals, one or more of which evolved into modern whales. *Ambulocetus* is characterized by such aquatic adaptations as a long tail and strong, paddle-like feet, but it still had land-mammal characters such as hooves on its toes and powerful jaws with shark-like teeth. It is related to *Indocetus* and *Dorudon* and is probably ancestral to *Rodhocetus* and *Basilosaurus*. Asia, Eocene.

Amebelodon a genus of large shovel-tusked proboscideans in the family Gomphotheriidae. About 10 feet high, *Amebelodon* was similar to *Platybelodon*, another shovel-tusker. See also ***Gnathobelodon***. Africa, Asia, and North America; late Miocene.

Ameridelphia a paraphyletic superorder of marsupials containing all American marsupials except *Dromiciops.* North and South America, early Paleocene to Recent.

Amia calva a carnivorous freshwater fish, commonly called bowfin. Notable especially for its primitive ganoid scales, it was once distributed globally but is now known only in the Great Lakes and Mississippi Valley. Paleocene to Recent.

Amiiformes an extant order of neopterygian fish generally placed with the Holostei. They were diverse and widespread from the Triassic through the Cretaceous but almost completely disappeared in the end-Cretaceous extinction. The only living representative is the bowfin, *Amia calva*. Global distribution, Triassic to Recent.

Ammonite a general term for ammonoid but sometimes also used to refer to the later ammonoids of the order Ammonitida.

Ammonitida and Ammonitina see **Ammonoidea**.

Ammonoidea a subclass of externally shelled cephalopod mollusks, notable for their hollow-chambered and coiled shells, generally with a ventral siphuncle. They had large eyes and captured prey with an array of tentacles. The ammonoids appeared in the Early Devonian and became important predators in the Paleozoic and Mesozoic seas, the last becoming extinct toward the end of the Cretaceous. The shells of almost all ammonoids follow a planispirally coiled pattern, but in the course of their 350 million years of existence, they developed a great diversity of patterns and ornamentation, especially in the late Mesozoic. There is some evidence of sexual dimorphism, with the females probably being larger. Spreading into all parts of the oceans, they were generally good swimmers, nektic or nektobenthic, and preying on smaller marine organisms. The ammonoids are the most important Mesozoic index fossils because of their wide geographic occurrence, their rapid diversification, and the persistence of a few genera through the Permian and Triassic extinctions.

Ammonoids' classification in orders and suborders is highly disputatious; the version given here attempts (probably in vain) to avoid controversy. They may be divided into eight orders, in order of appearance: (1) the Agoniatitida, Middle to Late Devonian, ancestral to all later ammonoids; (2) the Clymeniida, Middle to Late Devonian; (3) the Goniatitida, Middle Devonian to Late Permian; (4) the Prolecanitida, Late Devonian to Late Triassic; (5) the Ceratitida, Permian to Triassic; (6) the Phylloceratida, Early Triassic to Late Cretaceous; (7) the Lytoceratida, Late Triassic to Late Cretaceous; and (8) the Ammonitida, Early Triassic to Late Cretaceous. These eight groups may also be placed in three large orders, based mainly on their increasingly complex suture patterns: the Goniatitida, Ceratitida, and Ammonitida.

Two large suborders of the Ammonitida with intricately complex suture patterns, the Ammonitina and Ancyloceratina, are especially important biostratigraphically because of their generally short life-spans and wide geographic range. The Ammonitina appeared very early in the Jurassic and include 1000 known genera, organized in about 15 superfamilies. They typically follow the regular planispiral coiling pattern, with just a few heteromorph genera. The Ancyloceratina appeared in the Late Jurassic and persisted to the end of the Cretaceous, as the Ammonitina declined. They include many heteromorph genera of the Cretaceous, such as *Bostrychoceras*, *Hamites, Nipponites*, *Scaphites*, and *Turrilites*. Most were relatively short-lived, and they were probably weak swimmers because of their shape.

The earliest ammonoids evolved from unknown nautiloids near the beginning of the Devonian, but collection failure (scarcity of specimens of nautiloids at the end of the Silurian and in the Early Devonian and of the early ammonoids in the Devonian) leaves the connections unclear. The Phylloceratida (sometimes considered a suborder of the Ammonitida) probably gave rise to all post-Triassic ammonoids, such as the Lytoceratida. The Cretaceous ammonoids declined toward the end of the period, and the last disappeared in the end-Cretaceous extinction. See also **Nautiloidea** and **aptychus**.

Amniotes animals (including reptiles, dinosaurs, birds, and mammals) which evolved ways of protecting eggs inside the mother or at least inside a protective case. The basal amniotes were tetrapods that appeared in the Carboniferous about 312 Ma, descended from some group of reptiliomorphs such as the diadectomorphs or seymouriamorphs. (See ***Hylonomus*** and ***Paleothyris***.) Since they could reproduce independently of water, the appearance of amniotes was a crucial step in the development of terrestrial animal life.

Ampelocrinidae a disputed family of articulate crinoids usually considered cladids in the suborder Ampelocrinida. The Ampelocrinidae are sometimes mentioned as a possible stem group of the class Articulata. United States and England, Early to Late Carboniferous; possibly Australia and Thailand, middle to late Permian.

Amphechinus a genus of hedgehogs, small placental mammals in the extant family Erinaceidae. It appeared in Europe and Asia in the Oligocene and spread worldwide in the Miocene, becoming extinct at the end of the Pliocene.

Amphibamidae a family of temnospondyl amphibians in the superfamily Dissorophoidea. From 4 to 8 inches long, they are thought to be close to the ancestry of modern amphibians, but the connection is in dispute. Africa, United States, and Europe; Middle Pennsylvanian to Early Triassic.

Amphibia a diverse class of vertebrates, including two extinct groups, the Temnospondyli and the Lepospondyli, and one extant group, the Lissamphibia, which includes the frogs, toads, salamanders, and other smaller groups.

Amphichelydia an obsolete term for a suborder of cryptodire turtles.

Amphicyonidae a family of dog-like carnivorous mammals in the superfamily Arctoidea. Possibly also related to the Ursidae, they generally ranged from 10 to 200 pounds, but the largest species, *Amphicyon ingens*, is estimated to have weighed more than 1000 pounds. The Amphicyonidae achieved a holarctic distribution in the Oligocene but disappeared in the Pliocene; it is the only large family of post-Eocene carnivores that is not extant. North America, Europe, Asia, and Africa; middle Eocene to early Pliocene, 40–3 Ma.

Amphilestidae an enigmatic family of Mesozoic mammals in the order Eutriconodonta, related to the Morganucodontidae and Gobiconodontidae. Africa, Asia, Europe, and North America; Late Jurassic to Late Cretaceous.

Amphimerycidae a family of artiodactyl ruminants in the suborder Tylopoda. Restricted to Europe, late Eocene to middle Oligocene.

Amphineura see **Polyplacophora**.

Amphioxiformes see **Cephalochordata.**

Amphioxus an obsolete synonym for *Branchiostoma*; see **Cephalochordata**.

Amphipithecidae a family of early primates in the suborder Haplorrhini. It includes *Pondaungia* and the more recently discovered *Myanmarpithecus* and *Siamopithecus*. Known only from South Asia, middle to late Eocene.

Amphipithecus see ***Pondaungia***.

Amphisaurus see ***Anchisaurus***.

Amphisbaenia "going two ways," an extant group of mostly limbless reptiles in the order Squamata and superfamily Lacertoidea. Commonly called worm lizards, they also in some ways resemble snakes. From 4 inches to 2 feet long, they are basically insectivorous and live in burrows; most lay eggs but some species are viviparous. See, for example, **Rhineuridae** and ***Dyticonastis***. North and South America, Europe, Middle East, and Africa; Cretaceous to Recent.

Amphissites a large genus of straight-backed palaeocopid ostracods in the family Amphissitidae; global distribution, Carboniferous to Permian.

Amphistium paradoxum a species of pleuronectiform fish in the family Amphistiidae, one of the earliest ancestors of modern flatfish. Similar to *Heteronectes*, it represents a stage in the evolution of flatfish eye position, having one eye near the top of the skull. See also **flatfish.** Known only from Bolca, Italy, early to middle Eocene, 56–49 Ma**.**

Amphitheriida a poorly known order of early pantothere mammals in the clade Dryolestoidea. Scansorial insectivores, they were probably in the line of evolution toward placentals and marsupials. England, Middle Jurassic.

Amphiura plana an extinct species of ophiuroid burrowing brittle stars in the family Amphiuridae, known in Europe from the late Cenomanian to the end of the Cretaceous, 94–66 Ma.

Amphiuridae a diverse extant family of small ophiuroid brittle stars in the order Ophiurida. Global distribution, Jurassic to Recent.

Amphoracrinidae a family of cameratan crinoids in the order Monobathrida. Global distribution, Mississippian, 350–340 Ma.

Amphoracrinus a genus of crinoids in the family Amphoracrinidae. It is distinguished by a depressed cup and high tegmen surface. Europe and North America, Early Carboniferous, 345–343 Ma.

Amynodontidae a family of hornless perissodactyl mammals in the superfamily Rhinoceratoidea. Some genera resemble hippopotamuses in habit and appearance, while others have a tapir-like appearance. North America, Europe, and Asia; late Eocene to Pleistocene.

Anacleto Formation an Upper Cretaceous formation in Patagonia, known especially for the Auca Mahuevo site. The formation is dated between 84 and 78 Ma and has produced important dinosaur fossils. Argentina, Late Cretaceous.

Anactinotrichida see **Acari.**

Anagale a genus of early eutherian mammals in the order Anagaloidea. Rabbit-like in appearance, it was probably insectivorous, burrowing for beetle and worms. Mongolia, known only from the early Oligocene.

Anagenesis a concept briefly described as evolution within a lineage, while cladogenesis is evolution leading to a splitting of the lineage. Anagenesis is said to result in change in a species through a gradual accumulation of genetic and physical differences, without a branching off of a new species (cladogenesis). Anagenesis is considered the basic process involved in phyletic gradualism, while cladogenesis is basic to punctuated equilibrium.

Analogous structures body parts of different organisms that perform similar functions but are not necessarily built on the same anatomical plan. For example, wings of both insects and birds perform the same function and are analogous, but they are not homologous because they have no basic structural parts (such as bones) in common. See also **homologous structures** and **vestigial structures**.

Anancus a genus of large proboscideans in the family Gomphotheriidae and subfamily Anancinae. A forest browser 10 feet tall and weighing about 5 tons, *Anancus* had strikingly long tusks in the upper jaw, as long as 13 feet. Africa, Europe, and Asia; late Miocene to early Pleistocene.

Anapsid a term used to refer to reptiles that lack fenestrae behind the eye sockets in the skull. Traditionally, anapsids have been considered as one of five main subclasses of reptiles and as ancestral to diapsids and synapsids. The group is now recognized as paraphyletic or even polyphyletic, and the term is used only informally.

Anarcestes a genus of small ammonoids in the order Agoniatitida and family Anarcestidae, an important index fossil in the Eifelian Age of the Middle Devonian; Africa, Europe, Asia, and North America.

Anarcestida see **Agoniatitida**.

Anasca a polyphyletic extant group formerly considered a suborder of bryozoans in the order Cheilostomata. They are identified generally by the absence of an ascus (a water-filled sac with a hydrostatic function) in each zooid but are being reclassified into separate orders on the basis of other characters. Late Jurassic to Recent.

Anaspida an order of small, jawless, fish-like vertebrates usually considered agnathid ostracoderms. Although they had no more than a cartilaginous skeleton and only a weak headshield, some have an armor of deep, overlapping bony scales; they are also distinguished by a reversed heterocercal tail fin. Early Silurian to Early Devonian.

Anatolepis a possible early jawless fish, proposed as a heterostracan vertebrate, but *incertae sedis*, known only from tooth and carapace fragments; United States and Europe, late Cambrian to Early Ordovician.

Anatosaurus see ***Edmontosaurus*.**

Anatosuchus minor a small species of Cretaceous crocodiles, about 3 feet long and with a pointed, duckbill-like snout; Niger, 110 Ma.

Anchiornis huxleyi a species of small, birdlike theropod dinosaurs, generally placed in the Avetheropoda. Probably flightless, it was less than 2 feet long, with long legs, four toes, and proportionally large forelimbs. It was almost covered in feathers, some colored, according to researchers using melanosomes, cells that contain the pigment melanin. The color itself is not visible in the fossil, but electron-microscope analysis of follicle structure gives indirect evidence of color. Extrapolating from colors associated with the shape of the melanosomes in modern birds, researchers believe *Anchiornis* was covered with black and white plumage but also had a reddish crest of feathers. In the Yanliao biota, Tiaojishan Formation, China, Late Jurassic, 161 Ma.

Anchisaurus a genus of small basal sauropodomorph dinosaurs in the family Anchisauridae, formerly called *Megadactylus* and *Amphisaurus*. From 7 to 8 feet long and 60 to 80 pounds, it browsed on small palm trees and large shrubs. Known definitively only from the United States, Early Jurassic, 190–174 Ma.

Anchitherium a genus of horses in the extinct subfamily Anchitheriinae, related to *Mesohippus* and *Sinohippus*. About 2 feet high at the shoulder, it originated in North America in the Miocene and migrated to Asia, where it became extinct in the Pliocene.

Ancodonta a discarded term for a polyphyletic grouping of some primitive artiodactyl mammals.

Ancyloceratina "bent horn," a suborder of mostly heteromorph ammonoids in the order Ammonitida; see **Ammonoidea.**

Ancylopoda a suborder of perissodactyl ungulate mammals. Distinguished especially by their long, curving, cleft claws, most genera had forelimbs that were longer than the hindlimbs. The Ancylopoda include the eomoropids and the chalicotheres in the superfamily Chalicotherioidea. Holarctic distribution, Eocene to early Pleistocene.

Ancylotherium a genus of very large chalicotheres in the subfamily Schizotheriinae, about 7 feet tall and weighing as much as 1000 pounds; Europe, Asia, and Africa; late Miocene to early Pleistocene.

Ancyrocrinus a genus of crinoids in the order Cladida. With a stem 1–2 feet long, a small calyx, and long, branching arms, *Ancyrocrinus* is known for its unusual anchoring system, a sturdy holdfast in the shape of a grappling hook 1–2 inches wide. United States, Antarctica, Australia, and Europe; Early to Middle Devonian.

Ancyrodella rotundiloba a species of conodonts whose first appearance marks the beginning of the Frasnian epoch of the Devonian at 382.7 Ma. Its extinction in the great Frasnian Crisis, along with that of the conodont genus *Ozarkodina*, marks the boundary between the Frasnian and Famennian Ages of the Late Devonian at 372.2 Ma. France, Late Devonian.

Andalgalornis a monospecific genus of large, flightless predatory birds in the family Phorusrhacidae. Related to the larger *Kelenken*, *A. steulleti* was about 90 pounds and 4–5 feet tall and had a large, heavy skull with a deep hook on the upper jaw. Northwestern Argentina, Miocene to Pliocene.

Andreolepis a genus of actinopterygian fish, perhaps the earliest known. It has ganoid scales and has also been suggested as a stem-osteichthyan. It is known from several specimens of two species found in Scandinavia and Russia; late Silurian, 419–416 Ma.

Andrewsarchus mongoliensis a species of very large carnivorous or scavenging artiodactyl mammals in the clade Cetancodonta. Known only from a single skull almost 3 feet long, it was found by Roy Chapman Andrews, who estimated the body to have been about 12 feet long. It was formerly classed as a mesonychid but is now considered an artiodactyl, most closely related to hippopotamuses and whales. Mongolia, middle Eocene.

Anfesta stankovskii an obscure species of trilobozoans. Similar in shape to *Tribrachidium*, it was circular and less than an inch in diameter, with three straight radiating ridges. Russia, Ediacaran.

Angiosperms "vessel seed," the flowering plants, characterized principally by seeds enclosed in an ovary. Their ancestors have obscure roots in the Triassic (see ***Sanmiguelia***), and among the groups of early plants considered possible ancestors are the Nymphaeales, Amborellaceae, and the disputed order Illiciales. The first definitive angiosperms appeared in the Early Cretaceous and quickly spread worldwide. By the beginning of the Late Cretaceous, they were developing showy petals and layers of fruit to attract the insects and herbivores that were diversifying alongside the flowering plants that they fed on. As a result of this symbiotic lifestyle, the angiosperms have become the dominant plants globally since 100 Ma. See also ***Amborella***, ***Archaefructus*****, coevolution**, **Gnetales**, and ***Pluricarpellatia*****.**

Anguimorpha an extant clade of lacertilian squamates that contains several small families as well as the larger groups Varanidae and Anguidae, whose fossil record is

well-known from the Late Cretaceous (see, e.g., ***Odaxosaurus***, ***Varanus***, and ***Palaeosaniwa***).

Anhanguera a genus of pterodactyloid pterosaurs that flourished in Northern Brazil about 112 Ma. with a wingspan of up to 15 feet, *Anhanguera* is a close relative of *Ornithocheirus*, and like some other ornithocheirids, it had a pair of rounded crests at the top and bottom of a long beak. Known only from the Araripe Basin of Brazil, Early Cretaceous.

Animantarx "animated citadel," a monospecific mid-Cretaceous genus of ankylosaurian dinosaurs in the family Nodosauridae. About 10 feet long, *A. ramaljonesi* was heavily armored with bony scutes and horns but no tail club; it is known from only a single set of remains from Utah. United States, Early to Late Cretaceous, 104–98 Ma.

Anisograptid fauna see **Graptolithina.**

Anisoptera the dragonflies, a suborder of flying insects in the order Odonata. They are characterized generally by large compound eyes and two pairs of wings, the hindwings broader and slightly shorter than the forewings. They have slender but robust bodies and are strong fliers, differing from their close relatives the Zygoptera in several ways, chiefly in that they cannot fold their wings over the back. Global distribution, Jurassic to Recent.

Ankarapithecus meteai a species of fruit-eating apes that inhabited Asia Minor about 10 Ma. About 60 pounds, *Ankarapithecus* is known from a fragmentary male specimen found in 1950 and an almost complete face discovered in the 1990s. With some similarities to *Sivapithecus*, the finds are important because they are among the few primate fossils of the period between 18 Ma and 5 Ma. Turkey, late Miocene.

Ankylosauria a suborder of squat, small- to medium-sized ornithischian dinosaurs, containing the families Nodosauridae and Ankylosauridae. Most were protected by heavy armor: spikes on spine and neck; scutes on the body; and, for the Ankylosauridae, spiked tail clubs. See also ***Polacanthus***. Global distribution including Antarctica, Late Jurassic to Late Cretaceous.

Ankylosauridae a family of medium-sized ornithischian dinosaurs in the suborder Ankylosauria. Mainly herbivorous, squat, and quadrupedal, some grew to 20 feet long. Ankylosaurs are characterized by encasing armor plates, a fringe of pointed spines around the midriff of the body, and a spiked tail club; some species had plates even over the eyelids. North America, Europe, Asia, and Australia; Cretaceous, 125–66 Ma.

Annelida the phylum of segmented worms, including the subclasses Oligochaeta (earthworms) and Hirudinea (leeches), and the paraphyletic class Polychaeta

(bristle worms). Characterized chiefly by uniform, bilateral segmentation, most are terrestrial. The Polychaeta are marine invertebrates with a segmented body and many bristles; their chitinous jaws, called scolecodonts, are a widespread fossil from the Cambrian to the present.

Anodonta the duck or swan mussel, an extant genus of freshwater bivalves in the order Unionida and family Unionidae; North America, Europe, and Asia; Cretaceous to Recent.

Anodontosaurus lambei "toothless lizard," a genus of ankylosaurid dinosaurs in the subfamily Ankylosaurinae. Dated between 73 and 67 Ma, it is known from disarticulated specimens found in the Horseshoe Canyon Formation of Alberta. Medium-sized, armored, and herbivorous, it had a wide, pointed tail club. Canada, Late Cretaceous.

Anomalocarididae a family of soft-bodied animals of the early Paleozoic in the order Radiodonta. *Anomalocaris*, at 3–4 feet the largest predator in the Burgess Shale fauna, has been a contentious stem-arthropod for decades but is now well-known from widespread specimens, including some larger specimens in China and some from the Emu Bay Shale of Australia. Both its mouth and its body were at first incorrectly identified as separate animals, "*Peytoia*" and "*Laggania*," respectively, but *Peytoia* is now accepted as the name of another anomalocaridid, related to *Hurdia*. North America, Europe, Asia, and Australia; middle Cambrian to Early Devonian.

Anomocora see ***Coelosmilia***.

Anomodontia a clade of basal therapsids that includes especially the dicynodonts, the predominant herbivores in the late Permian. Global distribution, late Permian to Early Cretaceous.

Anomphalus a genus of marine vetigastropod snails in the superfamily Trochoidea and family Anomphalidae; type species *A. rotalus*. Global distribution, Early Devonian to Jurassic.

Anoplotheriidae a family of artiodactyl ungulate mammals in the suborder Tylopoda and extinct superfamily Anoplotheroidea. Related to camels, they were medium-sized forest browsers with long limbs and tails, along with a camel-like snout. Europe, Eocene to Oligocene.

Anoria a genus of medium-sized trilobites in the order Corynexochida and family Dolichometopidae, closely related to the slightly larger *Glossopleura*. From 3 to 4 inches long, it is known only from the Western United States, middle Cambrian.

Anoxia a chemical state characterized by a low level of oxygen, sometimes a complete lack of oxygen. Anoxic environments favor the preservation of fossils.

Anqingosaurus brevicephalus a species of iguanomorph lizards in the order Squamata, placed tentatively in the family Chamaeleonidae. The next oldest chameleon is *Chamaeleo caroliquarti* from the Miocene. China, early to middle Paleocene.

Anseriformes an order of waterfowl in the superorder Galloanserae. It includes many modern species as well as extinct groups such as the Gastornithidae and the earliest-known genus, *Vegavis*. Cretaceous to Recent.

Antarctodolops a genus of primitive marsupials in the family Polydolopidae. The only marsupial yet known from Antarctica, it is represented by the single species *A. dailyi*. Its discovery in 1982 bolsters the prediction that marsupials probably migrated from South America to Australia when the three land masses were still connected. Eocene to possibly Oligocene.

Antarctopelta oliveroi a species of ankylosaurian dinosaurs in the family Nodosauridae. About 13 feet long, it was the first nonavian dinosaur known from Antarctica. Although placed in the Nodosauridae, it seems to be a transitional form between the nodosaurs and ankylosaurs. Antarctica, Late Cretaceous, 84 Ma.

Anteaters see **Xenarthra**.

Antetonitrus ingenipes a species of sauropodomorph dinosaurs in the family Lessemsauridae, found in 1981 but only in 2003 recognized as one of the oldest sauropodomorphs known. About 30 feet long and almost 2 tons, *Antetonitrus* was one of the largest land animals of its time, although later sauropods came to weigh as much as 100 tons. It was quadrupedal but could also use its forelimbs for grasping objects. Found in the Elliot Formation along with ***Melanorosaurus***. See also **Vulcanodontidae**. South Africa, Late Triassic, 221–210 Ma.

Anthocyathea an abandoned name for a polyphyletic group of solitary, occasionally colonial, archaeocyathans with a roughly cylindrical cup and numerous bars, rods, and tabulae. Early to late Cambrian.

Anthozoa "flower animals," one of the three classes of cnidarians, including principally the corals; for the sea anemones, see **Actiniaria**. Corals are benthic marine animals that secrete corallite skeletons, often in conjunction with algae**.** The corallites of the Paleozoic corals (see **Rugosa** and **Tabulata**) were generally calcitic, while those of the modern corals (see **Scleractinia**) are almost all aragonitic. See also **Hexacorallia, Octocorallia**, and **Ceriantharia**. Global distribution, Cambrian to Recent.

Anthracosauria an obscure group of early amphibian tetrapods, probably paraphyletic, including the Embolomeri, Seymouriamorpha, and Diadectomorphs. Their classification is widely debated, but they are generally considered a stem group in the lineage leading to the amniotes. Late Devonian or Middle Mississippian to Early Triassic.

Anthracosia see ***Carbonicola***.

Anthracotheriidae a family of artiodactyl ungulates, probably related to hippopotamuses and whales. They were pig-like and probably semiaquatic, some genera the size of small hippos. See also ***Indohyus***. North America, Europe, Asia, and Africa; middle Eocene to late Pliocene.

Anthropoid an informal term referring to the monkeys, apes, and humans, generally replaced by more specific terms; see **Haplorrhini**, **Strepsirrhini**, **Catarrhini**, and **Platyrrhini**.

Anthropornis a genus of giant penguins almost 6 feet long; New Zealand and Antarctica, late Eocene to early Oligocene.

Antiarchi an order of small, heavily armored freshwater placoderm fish. The anterior body is armored, while the posterior is fish-like, and most antiarchs had a pair of small, moveable pectoral appendages. The order is well-known from the genera *Bothriolepis* and *Yunnanolepis*. Global distribution, early Silurian to Late Devonian.

Antilocapridae "goat antelope," the pronghorns, an extant family of ruminant artiodactyl mammals in the superfamily Giraffoidea. Very fast runners, they are second only to cheetahs in speed. Pronghorns are similar in size and shape to small antelopes but are more closely related to giraffes and okapis. They are distinguished from other artiodactyls by their permanent branching horns, which have a permanent bony core like that of bovid horns, with a horny sheath that is shed annually. Four genera are known from the early Miocene to the end of the Pleistocene, but the only living species is *Antilocapra americana*, ubiquitous in western North America since the Pleistocene. The Miocene genus *Ramoceros* had long, cervid-like forked horns with 3 or 4 tines, and other genera had a variety of horn configurations. Restricted to North America, early Miocene to Recent.

Antipatharia the black corals, an order of cnidarians in the subclass Hexacorallia. Poorly known, with a hard skeleton composed of unmineralized chitin and protein, so that its fossil record is enigmatic. The genus *Leiopathes* has been reported from the Miocene, and researchers in 2017 proposed two new species based on phosphatized fragments from the Fenxiang Formation of Southern China that show branches with long spines: *Sinopathes reptans* and *Sterictopathes radicatus*. Extant antipatharians, found generally in deep water, are slow-growing and are thought to

have a longer life-span than any other living animal. Cosmopolitan, Early Ordovician to Recent.

Ants see **Formicidae.**

Anura "tailless," the frogs, an enigmatic order of amphibians whose evolutionary history is unclear because of the paucity of their fossil record. The order includes the family Bufonidae, the toads. See **Proanura. G**lobal distribution, Jurassic to Recent.

Anurognathidae a family of small pterosaurs especially notable for evidence of a furry skin covering of pycnofibers. Only a few inches long and with a wingspan of 1–2 feet, they are among the smallest pterosaurs. The family includes *Jeholopterus*, *Anurognathus*, and several other genera. Europe, Asia, and possibly North America; Middle to Late Jurassic, 165–155 Ma.

Anzu wyliei a species of Late Cretaceous saurischian dinosaurs in the family Caenagnathidae. The largest oviraptorosaur of North America, it weighed about 650 pounds and was about 11 feet long and 10 feet high. It had a toothless beak and prominent crest and was probably feathered. Hell Creek Formation, North and South Dakota; late Maastrichtian, 66 Ma.

Apatemyidae a family of small Paleocene mammals in the extinct order Cimolesta and suborder Apatotheria. With long, hooked teeth, they were probably insectivorous and arboreal. North America and Europe, Paleocene to Eocene.

Apatornis "deceptive bird," a genus of flying birds in the family Apatornithidae. Generally considered neornithine and possibly close to the Anseriformes but known from only one fragment found in Kansas. United States, Late Cretaceous, 84 Ma.

Apatornithidae a contentious family of very early flying birds, generally placed in the order Ichthyornithiformes, the Cretaceous toothed birds. Their exact affinities, however, are still in question because of a paucity of specimens. It seems to have had a well-developed keel and other flight features. North America, Late Cretaceous.

Apatosaurus a genus of very large sauropod dinosaurs in the family Diplodocidae. With a long neck and a long, whip-like tail, it is estimated to have been up to 75 feet long and to weigh as much as 30 tons. See also ***Brontosaurus.*** North America, Late Jurassic, 152–151 Ma.

Apex Chert a formation in Western Australia containing microfossils that may be the oldest forms of life on Earth, dated at 3450 Ma.

Aphanosauria see **Avemetatarsalia.**

Aphrosalpingoidea an enigmatic superfamily of spongelike sessile animals generally classified as archaeocyathans. They had conical or cylindrical cups 1–2 inches wide. Europe, late Silurian.

Apidium a genus of anthropoid primates in the family Parapithecidae. Three species are known from the Fayum deposits of Egypt, early Oligocene, 30 Ma.

Apinae the bees, an extant subfamily of hymenopteran insects in the superfamily Apoidea. The taxonomic classification of bees is widely debated, but they are generally accepted as monophyletic, with Apinae including all genera of bees as well as several lesser-known insects. The earliest specimens are known from Early Cretaceous amber fossils (see ***Melittosphex***), with possible bee nests found in paleosols as far back as the Late Triassic. Along with other pollinating insects, bees spread globally alongside angiosperms in the early Late Cretaceous.

Apiocrinites a genus of Mesozoic pelmatozoan crinoids in the order Millericrinida. With a long, circular stem and a rigid, smooth, pear-shaped calyx, it had an unusually large holdfast. From 4 to 5 inches wide and a foot long, it was common in the Jurassic in shallow-water environments. North America, Europe, and Asia; Middle Jurassic to Late Cretaceous.

Apiocystites a genus of cystoid echinoderms in the class Rhombifera and order Dichoporita. It was sessile and 3–5 inches long and had massive thecae with complex plates. England and United States, middle Silurian to Early Devonian.

Aplacophora "bearing no shell," an extant class of benthic, deep-ocean mollusks. They are mostly small, from microscopic to 2 inches long, but a few grow up to several inches. Cylindrical and generally without shells (but see ***Kulindroplax***), and their body is covered with small aragonitic spicules. They are carnivorous, burrowing in the substrate or feeding on cnidarians. Global distribution, early Cambrian to Recent.

Aplodontia rufa a species of sciuromorph rodents in the family Aplodontiidae. Up to a foot long, with sharp claws, small eyes, and a very short tail, it is now found only in western North America. Known as the "mountain beaver," it is the only extant aplodontiid, although the family was widespread holarctically from the Oligocene to the Miocene. Pleistocene.

Aplodontiidae a family of sciuromorph rodents, closely related to the Sciuridae. The family flourished in North America in the Oligocene and spread across Eurasia to Europe but declined in the Miocene. Its only extant member is ***Aplodontia rufa***, *q.v.* Eocene to Recent.

Apodans see **caecilians**.

Apomorphy a derived trait, a novel specialized feature of an organism; see also **synapomorphy**.

Apsaravis ukhaana a species of primitive birds in the suborder Theropoda, a link in the chain of descent from dinosaurs to birds; Mongolia, Late Cretaceous, 80–75 Ma.

Apterous lacking wings.

Apterygote referring to wingless insects.

Apthoroblattina a genus of cockroaches in the extinct family Archimylacridae, about 2 inches long and 1.5 inches wide; North America, Europe, and Russia; restricted to Pennsylvanian.

Aptychus a curved calcitic or horny plate often found with ammonoids, sometimes attached to the body at the aperture. Its function is still debated, several possible uses having been suggested, the most likely being an operculum or part of a jaw. It is usually found singly but occasionally as a pair of aptychi. Its shape varies widely but is usually semicircular; since it is seldom found attached, the aptychus can seldom be assigned to a particular species. When found singly, it is sometimes called an anaptychus.

Arabidopsis thaliana thale cress, a living member of the mustard family, the Brassica, which includes cabbages and radishes; originally named *Pilosella siliquosa*, but the name has changed several times since. A model plant for genetic research, it is significant for having a small genome and for its genetic similarity to many other flowering plants, including corn, wheat, and rice. *Arabidopsis* offers further proof that the genes that control cell division are similar in plants and animals, supporting the inference that plants and animals originate from a common ancestor, probably a one-celled organism from about 1.5 billion years ago.

Arachnida a large class of arthropods in the subphylum Chelicerata. The most familiar order is the Araneae (spiders), and others are Scorpiones, Acari (ticks and mites), and the extinct Trigonotarbida. All arachnids have eight legs, although in some families, one pair has been converted to other functions. Early Silurian to Recent.

Araeoscelis a genus of small, lizard-like diapsid reptiles in the order Araeoscelida, similar to *Petrolacosaurus* of the Late Pennsylvanian. About 2 feet long with a tail as long as its body, it was one of the earliest diapsids but was exceptional in that both parts of one pair of temporal fenestrae were closed with bone. United States (Texas), early Permian.

Aragonite a polymorph mineral of calcium carbonate, chemically identical to calcite but with an orthorhombic crystal structure, different from calcite's rhombohedral structure. Aragonitic mollusk shells fossilize less readily than calcite shells because of their unstable structure, resulting in gaps in the fossil record. Aragonite commonly recrystallizes as calcite over time and is less common in older fossils.

Arandaspis a genus of jawless heterostracan fish in the order Pteraspidiformes. Dated at 465 Ma, it is considered by some the earliest vertebrate. It was 6–8 inches long and finless and was armored with large bony plates and straps rather than with the tiles seen in its cousin *Astraspis*. Australia and South America, Middle Ordovician.

Araneae the true spiders, an extant order of arachnids with eight legs and cheliceral venom glands; most have spinnerets that produce silk. There are two extant suborders, both known from the Carboniferous to the present. Most spider families and genera are included in the Opisthothelae; the other suborder is the smaller and more primitive Mesothelae, with several representatives from the Carboniferous. The Araneae diversified greatly in the Jurassic, but the fossil record is sparse, and 90 percent of the known spider fossils are in amber from the Cenozoic, difficult to study. Fossil specimens of their webs are sometimes found because of insects trapped in them, the earliest-known being fragments of a spider web (140 Ma) in a piece of amber from Sussex, England (140 Ma), and a complete orb web with prey attached (a fly, a mite, a beetle, and a wasp leg) in amber from Spain (136 Ma). Global distribution, Carboniferous to Recent.

Araneidae the orb-weaver spiders, the principal family in the superfamily Araneoidea. Cosmopolitan, Early Cretaceous to Recent.

Araneoidea the larger of the two extant superfamilies of araneomorph orb-weaving spiders. Most araneoids possess spinnerets and other morphological synapomorphies connected with web-spinning, weaving webs of adhesive threads as opposed to the cribellate silk of the **Deinopoidea**, q.v. The discovery of some early cribellate araneoids (e.g., *Juraraneus*) seems to indicate that the ecribellate condition may have evolved more than once. Global distribution, middle Paleozoic to Recent.

Araneomorphae an extant clade of spiders in the suborder Opisthothelae. The great majority of spiders are araneomorphs; they are distinguished especially by their pincer-like fangs and by their short life-span, most dying after a year. Their fossil record is almost nonexistent, but see **Archaeidae**, ***Argyrarachne***, ***Hypochilus*****,** and ***Triassaraneus***. Global distribution**,** Triassic? to Recent.

Araripe*mys* a genus of early turtles in the order Testudines and extinct family Araripemydidae or Pelomedusidae. The type species *A. barretoi* is not well-known but is estimated at 2 feet long. Brazil, Early Cretaceous.

Araripe Plateau and Basin a region in Northeast Brazil that has produced a large and diverse fossil assemblage of plants and animals from the Early Cretaceous, before South America split off from Africa. See **Crato** and **Santana Formations**.

Araripesuchus gomesii the type species of *Araripesuchus*, a notosuchian crocodyliform of Gondwana. A short-snouted crocodilian about 2 feet long, it is found in the Santana Formation of the Araripe Basin. Brazil, Early Cretaceous.

Araripesuchus rattoides the second African species of *Araripesuchus* to be found. About 3 feet long and notable for its buckteeth, which it used to root in soil for grubs and plants, it probably spent most of its time on land. Morocco, Early Cretaceous.

Araripesuchus tsangatsangana the geologically most recent *Araripesuchus*, dated at 66 Ma; Madagascar, Late Cretaceous.

Araripesuchus wegeneri the first African species of the genus. About 3 feet long and omnivorous, it ran on long legs like a dog and swam well with a long crocodilian tail. Niger, Early Cretaceous.

Araucaria a genus of plants in the extant family Araucariaceae, distantly related to pines. Several genera have existed almost unchanged for hundreds of millions of years and are considered "living fossils," such as the Norfolk Island pine (*A. heterophylla*) and the monkey puzzle tree (*A. araucana*), which is known from as far back as 250 Ma. *Araucaria* appeared in the Early Triassic and diversified rapidly worldwide, creating forests of trees as tall as 250 feet. Triassic to Recent.

Araucariaceae an extant family of coniferous trees in the class Pinopsida and order Pinales. Appearing in the Early Carboniferous, they spread worldwide in the Mesozoic but disappeared in Laurasia at the end of the Cretaceous. A notable site for them is Petrified Forest National Park in the Southwestern United States. Global distribution, Carboniferous to Recent.

Arborea a genus of Ediacaran organisms tentatively placed in the proposed clade Arboreomorpha. Its frond-like body was 3–4 inches long and was attached to the substrate by a holdfast consisting of concentric circles. Similar to *Charniodiscus*, it was so first named. Australia and Russia, late Ediacaran.

Arcestidae a family of ammonoids in the order Ceratitida, generally broad and rounded, with an unusual spherical shape. Its type genus, *Arcestes*, was especially widespread. Global distribution, late Permian to Late Triassic.

Archaea one of the three basic domains of life forms, a group of prokaryotes, single-celled organisms without a defined nucleus. Distinguished from bacteria, the other prokaryotic domain, by some eukaryotic genes and metabolic characteristics. Notable for tolerance of extreme environments, many of them live near hydrothermal

vents in the ocean floor. The earliest-known fossilized Archaea date back to 3.5 billion years ago, but genetic research indicates that they probably originated closer to 4 billion years ago. See also **Bacteria** and **Eukaryota**.

Archaefructus liaoningensis the best known of three species of a genus of early (125 Ma) flowering plants in the Jehol Biota, proposed as stem-group angiosperms but still poorly known; China, Early Cretaceous.

Archaeidae a small family of araneomorph spiders. Their most notable feature is elongated and highly maneuverable jaws, adapted for preying on other spiders. They are known sparsely in the fossil record, and only from European and Burmese amber specimens. Cosmopolitan, now known only in Southern Africa, Madagascar, and Australia; Jurassic to Recent.

Archaeocalamites a genus of the earliest-known horsetails in the order **Calamitales** (*q.v.*); Pennsylvanian to Permian.

Archaeoceratops a genus of basal neoceratopsian dinosaurs in the family Archaeoceratopsidae. Only 3 feet long, it had no horns or neck frills but had a large skull and a small bony frill near its tail. The type species *A. oshimai*, the earliest-known neoceratopsian, is dated at about 125 Ma. China, Early Cretaceous.

Archaeoceti a paraphyletic suborder of ancestral cetaceans. Fish-eating and dolphin-like, they grew up to 33 feet long and had at least vestigial hindlimbs and an elongated snout. The earliest are known from the island continent of India in the early Eocene (see ***Pakicetus*** and ***Ambulocetus***), and they diversified rapidly worldwide. Early Eocene to late Oligocene.

Archaeocidaris a genus of early euechinoids in the extinct order Cidaroida; global distribution, Late Devonian to late Permian.

Archaeocopida see **Bradoriida**.

Archaeocyatha "ancient cups." The archaeocyathans were sessile and spongelike marine organisms, mostly solitary but some colonial. Their classification has shifted considerably over time, the current consensus placing them with the hypercalcified sponges. Among the earliest reef builders, they were solitary or colonial, generally cup-shaped or conical, with two layers of perforated calcareous walls, mostly between 1 and 6 inches tall. Prominent in the Tommotian biota, they were worldwide and highly diverse index fossils for the early Cambrian but began to decline by the middle Cambrian. Most genera had disappeared by the end of the Cambrian, and the last-known species, *Antarcticocyathus webberi*, became extinct just before the end of the period. After the disappearance of Archaeocyatha, there were almost no reef-building animals until the rise of the Late Ordovician reef builders such as the stromatoporoids and stenolaemates 50 million years later.

Archaeocyon a genus of small canids, the earliest-known member of the extinct subfamily Borophaginae. The omnivorous, fox-sized *Archaeocyon* was up to 2 feet long and weighed 3–4 pounds. Western North America, early to late Oligocene.

Archaeodelphis patrius a species of stem-odontocete whales placed tentatively in the family Xenorophidae, known only from a single partial specimen; Southeastern United States, late Oligocene.

Archaeodontosaurus descouensi a species of sauropod dinosaurs with prosauropod-like teeth, found in 1999 and dated at 168 Ma. Known only from bone fragments and teeth, it is estimated to have been 40 feet long. Madagascar, Middle Jurassic.

"Archaeogastropoda" an extant paraphyletic group of sea snails and limpets, prosobranch gastropods that first appeared in the Cambrian and have been very widespread and diverse since a mid-Paleozoic radiation. In recent reclassifications of the gastropods, the term has been dropped, with members of the group now placed mainly in the Patellogastropoda and Vetigastropoda.

Archaeognatha an extant order of apterygote insects, also called Microcoryphia and previously considered part of the now obsolete order Thysanura. Among the most primitive insects, they appeared about 390 Ma. They are characterized by a long, slender body, arched back, and two cerci and a medial extension on the tail. Cosmopolitan, Middle Devonian.

Archaeolepis mane a species of lepidopteran insects in the family Archaeolepidae. It is the earliest-known lepidopteran, identified from wings found in an Early Jurassic stratum in Dorset, England, 190 Ma.

Archaeolynthus a genus of primitive archaeocyathans in the order Monocyathida. Solitary or colonial and branching, the small, single-walled *Archaeolynthus* was one of the simplest archaeocyathans. Cosmopolitan, Cambrian.

Archaeopteris "ancient feather," a genus of progymnosperm trees in the order Archaeopteridales. Growing up to 25 feet high, *Archaeopteris* created the first large forests in the Devonian and was an important ancestor of later plants. *Archaeopteris* had fern-like true leaves and was similar to modern trees in its branching growth pattern; its significant characteristics include heterospory and dense gymnospermic secondary wood. Global distribution, Late Devonian to Early Carboniferous.

Archaeopteryx a genus of the earliest-discovered feathered theropods, generally considered transitional between dinosaurs and modern birds. *Archaeopteryx* is known principally from a dozen specimens from the Solnhofen Limestone quarry in central Bavaria and dated at 150 Ma. It was about the size of a raven and was a weak flyer, probably incapable of launching into flight from the ground. Its features seem

half-reptilian (teeth, a long tail of vertebral bones, and claws on its wings) and half-avian (a birdlike beak; long feathers on wings capable of some flight; and a hallux facing to the side or rear, adapted to grasping a tree branch). More modern bird physiology seems to have first appeared in later feathered dinosaurs found in China and dated about 130 Ma. Europe, Late Jurassic.

"Archaeoraptor liaoningensis" one of several fake fossil specimens produced in China in recent decades, supposedly a turkey-sized feathered dinosaur capable of flight. Publicized in 1999 by *National Geographic*, it was soon discovered to be a composite of bones from different animals; the magazine published a full retraction later, but the hoax has joined Piltdown Man as one of the most famous frauds in the history of science. Many genuine feathered dinosaurs have been found since then, mostly in China, now undergoing a much more thorough investigation than in the 1990s.

Archaeornithomimus a genus of coelurosaurian theropod dinosaurs in the family Ornithomimidae. About 11 feet long and probably omnivorous, *Archaeornithomimus* is known from disarticulated skeletal specimens of several individuals. Asia, Late Cretaceous, 75–66 Ma.

Archaeotherium a genus of artiodactyl mammals in the family Entelodontidae. With a long, flanged skull and grooved canine teeth, *Archaeotherium* was omnivorous but mainly a scavenger. Bison-sized, it looked like a giant warthog, closely resembling its later relative *Daeodon*. North America, late Eocene to late Oligocene.

Archaeothyris a genus of small, lizard-like synapsids in the family Ophiacodontidae. Less than 2 feet long, *Archaeothyris* resembled a small iguana. The three known specimens are dated between 311 and 307 Ma, and it is the earliest accepted synapsid, but see also ***Echinerpeton***. North America and Czech Republic, Late Carboniferous.

Archanodon catskillensis a genus of large bivalves in the order Unionida. It is the earliest-known freshwater bivalve. United States, Middle Devonian.

Archelon "ruling turtle," a monospecific genus of marine turtles, generally placed in the extant suborder Cryptodira and extinct family Protostegidae. It is the largest-known turtle, about 13 feet long and 16 feet wide flipper to flipper; it probably weighed about 2 tons. Instead of the solid shell of most modern turtles, *A. ischyros* had a skeletal framework with bony rib struts that supported a leathery carapace. United States, Late Cretaceous, 80 Ma.

Archeria a genus of primitive anthracosaurians in the family Archeriidae. About 7 feet long, it was an aquatic eel-like predator and is notable for being known from one of the few almost complete skeletons of its type. United States (Texas and Oklahoma), early Permian.

Archicebus achilles the earliest-known haplorrhine primate, an almost complete specimen discovered in China around 2005. About 9 inches long, including a 5 inch tail, it weighed only an ounce. Probably arboreal, it is notable for a distinctive heel bone and marmoset-like teeth. China, early Eocene, 55 Ma.

Archimedes a genus of stenolaemate bryozoans in the order Fenestrida and family Fenestellidae. Very different in appearance from other fenestellids, *Archimedes* is named for its shape, which closely resembles an Archimedes screw. They formed upright colonies up to 3 feet high, with a fenestrate network at the edges of the screw. Global distribution, Middle Mississippian to middle Permian.

Archipolypoda a superorder of millipedes in the subclass Chilognatha, possibly the earliest terrestrial animals; Europe and North America, Silurian to Late Carboniferous.

Architarbus a genus of phalangiotarbid arachnids in the family Architarbidae. The spider-like *Architarbus* had an oval body 3–4 inches long, with a broadly joined cephalothorax. United States and Germany, Middle Pennsylvanian.

Archonta see **Euarchonta**.

Archosauria a clade of advanced diapsid reptiles including modern crocodiles and birds as well as the extinct pterosaurs and dinosaurs. The earliest archosaurs were the Proterosuchidae, which appeared near the end of the Permian and diversified rapidly in the Early Triassic. The archosaurs were widespread and dominant throughout the Mesozoic, but only a few families survived the mass extinction at the end of the Cretaceous. Global distribution, Permian to Recent.

Arcovenator a monospecific genus of ceratosaurian theropod dinosaurs in the family Abelisauridae. *A. escotae* is known only from a partial skull but seems to have most of the abelisaurid characters. Dated at 74 Ma, it was probably part of a northward migration of the Gondwanan abelisaurs toward the end of the Cretaceous. France, Late Cretaceous.

Arctocyonidae a large, possibly polyphyletic family of primitive, unspecialized mammals. Ranging in size from raccoon-like (*Chriacus*) to bearlike (*Mentoclaenodon* and *Arctocyon*), the group presents a combination of carnivore and ungulate characteristics. North America and Europe, Late Cretaceous to early Eocene.

Arctodus a genus of large and very long-limbed bears in the still-extant subfamily Tremarctinae. *A. simus*, the Great North American short-faced bear, was larger than the modern grizzly, 4 to 5 feet high at the shoulder and weighing almost a ton. North America, Pleistocene.

Arctolepis a genus of early arthrodire placoderm fish in the family Phlyctaeniidae; synonym *Acanthaspis*. Less than a foot long, it is characterized especially by its long and stout pectoral fins and by its heavy anterior armor. United States and Europe, Early to Middle Devonian.

Arctotypus a genus of griffinflies in the order Meganisoptera, with a compact and relatively heavy body, and a wingspan of about 12 inches; Europe and Asia, Carboniferous to Permian.

Arcyzonidae a family of palaeocopid ostracods in the superfamily Kirkbyoidea, distinguished by a central pit on each valve; known only from China, Early Devonian.

Ardipithecus "ground ape," *Ar. ramidus* is a species of hominin known principally from a partial female skeleton found in 1992 in the Middle Awash region of Ethiopia, dated about 4.4 Ma. *Ardipithecus* is closely related to the last ancestor shared by chimpanzees and humans, and it may be a direct ancestor of the australopithecines.

Ardipithecus was omnivorous, not just a frugivore, and had a flexible palm and possibly bipedal feet, although it had good climbing ability and may have nested in trees. Ardipithecus was about 4 feet tall, weighed about 120 pounds, and had good grasping ability in hands and feet, including an opposable big toe. Several questions remain about its classification and its bipedality. Discovered in a more heavily forested area than most hominid skeletons, *Ardipithecus* may have been able to walk bipedally but was also at home in the trees.

A partial skeleton whose skull was in coin-sized pieces is kept in the National Museum of Ethiopia. A second possible specimen, dated between 5.8 and 5.2 Ma and named *Ar. kadabba*, is known from teeth and several skeletal bones. Miocene to Pliocene.

Argentavis a monospecific genus of very large predatory and scavenging birds in the family Teratornithidae; weighing up to 170 pounds, *A. magnificens* had a wingspan of about 23 feet, similar to the smaller seabird *Pelagornis sandersi*; Argentina, late Miocene.

Argentinosaurus huinculensis one of the largest land animals known, a species of titanosaurian sauropod dinosaurs. Although only a few vertebra and other bones have been found, *A. huinculensis* may have weighed 100 tons and reached more than 120 feet in length, with a long neck and tail. See also **Titanosauria, *Patagotitan*,** and ***Puertasaurus***. Patagonia, Late Cretaceous, 97–94 Ma.

Argyrarachne solitus a species of Triassic spiders probably in the clade Araneomorphae, from the Solite Quarry. The specimen is fairly well-preserved, showing fine details such as a covering of setae on long, slender legs as well as a subrectangular carapace and short, dentate claws; nevertheless, it is not complete

enough to allow definitive classification. United States, Late Triassic (Carnian), between 226 and 220 Ma.

Arkanites a genus of goniatitic ammonoids in the family Reticuloceratidae. Related to *Retites* and *Quinnites*, it is subglobose, with prominent ribbing and deep grooves. Known only from the Midwestern United States, Early Pennsylvanian.

Arkarua an Ediacaran genus tentatively placed in Echinodermata but still of uncertain relationships, perhaps related to the trilobozoans. Known only from a cast half an inch in diameter, it has a raised center with pentameral symmetry. Its design resembles that of *Tribrachidium*, but with five arms rather than three. Australia, Ediacaran.

"Arpylorus antiquus" a supposed species of protists long considered a possible early dinoflagellate but rejected in 2012, being designated as simply part of a more complex organism.

Arretosaurus ornatus a species of iguanomorph lizards in the order Squamata and family Arretosauridae. Considered a possible early chameleon but still *incertae sedis*. China, early Oligocene, 34–28 Ma.

Arsinoitherium a genus of large paenungulate mammals in the order Embrithopoda and family Arsinoitheriidae, known mainly from complete skeletons found in the Fayum Depression. Growing up to 10 feet long, they are related to elephants despite having a very different skull, which bears two very large bony horns extending forward from its nose. Possibly related specimens have also been found in Europe and Mongolia. Egypt and Arabian Peninsula, Eocene to Oligocene.

Arthrodira the most successful order of placoderms, characterized especially by a ball-and-socket neck joint that allowed the head to rise, enlarging its gape. Generally armored and at first only a few inches long, many became very large during the Devonian, reaching a length of 30 feet in *Dunkleosteus*. The arthrodires were among the dominant predators of the Devonian until their extinction at the end of the period. Global distribution, Early to Late Devonian.

Arthropleura a genus of large Paleozoic millipedes in the extant subphylum Myriapoda and the extinct subclass Arthropleuridea. Arthropleurids were 1–7 feet long and up to a foot wide, the larger species being the largest terrestrial invertebrates known. North America and Europe, Carboniferous to early Permian.

Arthropoda "jointed foot," the largest phylum of animals, including about 80 percent of all described extant species. Characterized basically by a segmented body, jointed appendages, and an exoskeleton (a chitinous cuticle). Among its subphyla are trilobites, crustaceans, myriapods, chelicerates, and hexapods (the insects). Early Cambrian to Recent.

Articulata (crinoids) the only extant subclass of crinoids. It includes the extant orders Bourgueticrinida, Comatulida, Cyrtocrinida, Isocrinida, and Millericrinida. The origins of the Articulata are obscure (see **Ampelocrinidae** and **Cymbiocrinidae**), but they are generally thought to have appeared in the Triassic, evolving from uncertain ancestors that survived the end-Permian extinction. Possible stem-Articulata genera of the Early Triassic have been suggested from the Holocrinidae and Encrinidae.

Articulate of brachiopods and bivalves, using teeth or sockets to hold valves together, as opposed to using muscles to secure the joint in the manner of inarticulate species.

Articulation a connection between parts of the structural framework of an organism, usually a joint between parts of the skeleton.

Artiodactyla an order of herbivorous hoofed mammals with an even number of toes, the most successful group of large mammals. Evolved from condylarths, the group includes most large land mammals, such as the pig, sheep, hippopotamus, pronghorn, deer, cow, giraffe, camel, llama, and bison, and dozens of species of antelope. Since the cetaceans (whales, dolphins, and porpoises) evolved from early even-toed ungulates, they are also considered to belong with artiodactyls in the clade Cetartiodactyla**.** See also **Perissodactyla**. Early Eocene to Recent.

Asaphida a very large order of trilobites, included in the proposed subclass Librostoma. The asaphids account for about 20 percent of the known trilobite species. Although the order includes a great number of disparate shapes and sizes, its members are generally isopygous and have a prominent ventral suture. The superfamily Asaphoidea is also recognized by prominent eyestalks. The asaphids declined at the end of the Ordovician, with only one of the six superfamilies, the Trinucleoidea, surviving into the Silurian. Global distribution, middle Cambrian to late Silurian.

Asaphus a genus of large trilobites in the order Asaphida and family Asaphidae. Isopygous and rounded, it grew up to 3 inches long, with prominent holochroal eyes. Several species (e.g., *A. kowalewski*) had long eyestalks. Cosmopolitan, Middle Ordovician to early Silurian.

Ascidiacea a paraphyletic class of soft-bodied animals in the subphylum Tunicata. Because of their scanty fossil record, there are only a few reliably identified fossils. The oldest reported is from the early Cambrian Chengjiang biota of China. Among the later definitive fossil specimens are some specimens from the Jurassic and the extant genus *Cystodytes*, known from the Eocene. Global distribution, early Cambrian to Recent.

Ascomycota "sac fungus," the largest division of the kingdom Fungi. Distinguished by a spore-producing ascus, they are known from Devonian fossils but are believed to be much older.

Asilisaurus kongwe a species of very early dinosauriform archosaurs, generally placed in the family Silesauridae. Known only from partial and fragmentary remains, *A. kongwe* was quadrupedal, possibly herbivorous, and 3–10 feet long and weighed as much as 65 pounds. Described in 2010, it displays several dinosaurian traits and is generally considered the earliest-known dinosauriform. Tanzania, Middle Triassic, 245 Ma.

Asioryctitheria a proposed order of basal eutherian mammals; insectivorous and probably the earliest modern mammals. The order includes the genera *Asioryctes* and *Kennalestes* and the proposed genera *Sasayamamylos* and *Ukhaatherium*. China and Japan, Early to Late Cretaceous.

Aspidella terranovica an enigmatic species of discoidal fossils of the late Precambrian. Best known from the Ediacaran fauna of Canada, it is variously considered a stem-animal, an alga, or a lichen. Generally 3–4 but up to 7 inches wide, it has a concentric ring structure and may be the imprint of an anchoring disc of an organism with fronds. See also ***Charnia*** and ***Medusinites***. Canada, United States, Kazakhstan, and Australia; Ediacaran.

Aspidorhynchiformes a Mesozoic order of actinopterygian fish in the subclass Neopterygii. About 2 feet long with an elongated and tooth-lined jaw, they superficially resemble the modern gars but are not related. North America, Europe, and Asia; Middle Jurassic to Late Cretaceous.

Asteraceae the largest family of angiosperm plants. Also called Compositae, they had composite flowers with flowering heads surrounded by bracts. Late Cretaceous to Recent.

Asteroidea the sea stars or starfish, a class of asterozoan echinoderms. The central body has radial symmetry, extending into five or more arms that are not sharply marked off from the body. Since sea stars disintegrate quickly after death, the fossil record is weak. Global distribution, Ordovician to Recent.

Asterozoa a subphylum of echinoderms; see **Asteroidea** and **Ophiuroidea**.

Astogeny the growth and development of colonial organisms such as corals; see also **ontogeny**.

Astrapotheria an order of hoofed mammals in the superorder Meridiungulata. Up to 10 feet long, the larger species resembled a small, tapir-like mastodon, with long, tusk-like canines. *Trigonostylops* is a smaller Eocene version, and the Miocene *Astrapotherium* is the type genus. South America and Antarctica, Paleocene to Miocene.

Astraspis a genus of jawless fish in the subclass Astraspida related to *Arandaspis*. *Astraspis* grew to about 8 inches long and was armored with bony tiles, which on its head were somewhat star-shaped. North and South America, Middle Ordovician.

Astrophic see **strophic.**

Atacamatitan chilensis name given in 2011 to a species of titanosaurian sauropod dinosaurs, possibly related to the Nemegtosauridae. Originally called *Domeykosaurus*, it is poorly known from skeletal fragments first described in 2003 and dated near the end of the Cretaceous. Northern Chile, Late Cretaceous.

Atelostomata a superorder of irregular echinoids that includes the orders Holasteroida and Spatangoida. They have no lantern and are microphagous feeders, finding particles of food on the substrate. Global distribution, Early Jurassic to Recent.

Athyridida an order of articulate brachiopods in the class Rhynchonellata, characterized by biconvex, smooth, and impunctate shells with laterally directed spires. Global distribution, Late Ordovician to Jurassic.

Atlanthropus mauritanicus see **Ternifine Man**.

Atlasaurus imelakei a species of sauropod dinosaurs. Known only from an almost complete skeleton found in Morocco, it is estimated at about 50 feet long and 26 tons. *Atlasaurus* is related to the larger *Brachiosaurus* but has a shorter neck and comparatively larger skull; its spoon-shaped teeth have denticles. Morocco, Middle Jurassic.

Atrypa a genus of articulate brachiopods in the order Atrypida and family Atrypidae. Up to 1.3 inches in diameter, *Atrypa* had a round, impunctate shell with many fine ridges. The pedicle valve is convex except that it may transition to concave toward the anterior edge; the brachial valve is strongly convex. Global distribution, early Silurian to Early Carboniferous.

Atrypida an order of articulate brachiopods in the class Rhynchonellata. Often massive or nut-shaped, generally 1–2 inches in diameter, the impunctate shell has a short hinge line and typically has fine rays and growth lines. The atrypids were the first brachiopods to develop a spiral lophophore. They diversified widely in the

Silurian and Devonian, almost disappearing in the Frasnian extinction near the end of the Devonian but surviving in a few locations to the Early Carboniferous.

Attenborites janeae a species of Ediacaran organisms described in 2018. Less than a third of an inch long, it is egg-shaped and ridged, and was probably planktic. Flinders Ranges, Australia, 550 Ma.

Attercopus a monospecific genus of arachnids in the order Uraraneida. *Attercopus fimbriunguis*, the earliest-known proto-spider, had the primitive feature of a flagellum-like tail as well as spider-like characteristics. It did not have spinnerets but produced silk from silk gland openings in the abdomen, probably using it only to line burrows or wrap eggs. See also ***Permarachne*****.** United States (New York); Middle Devonian, between 388 and 383 Ma.

Aturia a genus of nautiloids in the order Nautilida, the only genus in the family Aturiidae. It is discoidal, involute, and smooth-shelled and has a very complex suture pattern. Cosmopolitan, early Paleocene to late Miocene.

Auca Mahuevo the name of a remarkable site in Patagonia that includes an extensive dinosaur nesting area with very well-preserved eggs, some with embryos inside. Some embryos are very well-preserved, some even including skin specimens. The nests and the remains of many large titanosaurian dinosaurs indicate that Auca Mahuevo was a nesting site for thousands of years. It extends over several square kilometers, and nests and skeletons have been found at several different levels of deposition. Argentina, late Cretaceous, 84–80 Ma.

Augustynolophus a monospecific genus of hadrosaurid dinosaurs in the subfamily Saurolophinae; synonym *Saurolophus morrisi*. Known from a skull, vertebrae, and limb bones, *A. morrisi* was the first dinosaur found in California, near Fresno. United States, late Maastrichtian.

Aulacostephanidae a family of ammonitid ammonoids in the superfamily Perisphinctoidea. Several species are significant index fossils for the Kimmeridgian of the Late Jurassic, 157–152 Ma. Global distribution.

Aulacothyris a genus of punctate articulate brachiopods in the superfamily Zeillerioidea. They are characterized by a long loop and a convex pedicle valve with a strikingly large fold along the posterior to anterior plane. Europe, restricted to Middle Jurassic.

Aulacocerida the oldest coleoids, an order of cephalopods in the subclass Belemnoidea; global distribution, Devonian to Late Jurassic.

Aulolepis a genus of teleost neopterygian fish in the small extinct order Ctenothrissiformes. It had a short, deep body and a large dorsal fin. Europe, Late Cretaceous, late Cenomanian, about 95 Ma.

Aulophyllum a genus of solitary rugose corals in the order Stauriida and family Aulophyllidae; it is closely related to *Dibunophyllum*. *Aulophyllum* was trochoid and often large; its dissepiments are small and concentric. It is best known from Scotland but also occurs in the United States, Europe, Russia, and Africa; Early Carboniferous.

Aulopora an order of colonial tabulate corals in the extinct family Auloporidae. They were marked by cylindrical corallites in a branching tubular structure, encrusting a hard substrate. Global distribution, Ordovician to Permian.

Aurornis xui An enigmatic species of birdlike dinosaurs in the family Anchiornithidae. Known from one specimen with uncertain provenance, it was about 20 inches long and had small, sharp teeth. It was probably flightless but had long, winglike arms and was covered with feathers. Late Jurassic or Early Cretaceous.

Australasia a geographic region including Australia, New Zealand, New Guinea, and smaller neighboring islands.

Australidelphia a superorder of marsupials that contains all of those from Australasia and one from South America (see ***Dromiciops***). Late Paleocene to Recent.

Australopithecus a genus of primates in the family Hominidae. With specimens spanning the period from 4.4 to 1.5 Ma, the australopithecines are among several possible ancestors of the genus *Homo*. They exhibit both human and ape characteristics, with a cranial capacity of around 600 cc. Some authorities have classified them in two types, "robust" and "gracile," but the continuing variety exhibited by newly found specimens indicates that there was a wide range of types of australopithecines and other early hominins living in East Africa at the time. In addition to the five species mentioned here, other proposed species named so far include *Au. boisei*, *Au. garhi*, *Au. paranthropus, Au. prometheus, and Au. robustus.*

Australopithecus afarensis the best-known species of australopithecines, known from remains of several individuals, including the famous specimen named Lucy. Found in East Africa, particularly near the border of Ethiopia and Tanzania, the remains have generally been dated as being between 3 and 4 million years old. Research indicates that *Au. afarensis* could walk upright because the foot bone exhibits an arch similar to that of modern humans. See also **Middle Awash.**

Australopithecus africanus a well-known species of australopithecines, known principally from several sites in Southern Africa. Although anatomically similar to *Au. afarensis*, it had a larger brain and smaller teeth. *Au. africanus* is probably not a direct ancestor of *Homo sapiens*. Since most of the specimens were found in caves, its dating is problematic, but it probably lived between 3.3 and 2.1 Ma.

Australopithecus anamensis an early australopithecine, known from specimens found in the Middle Awash and in Kenya; about 4.1 Ma.

Australopithecus bahrelghazali a species of australopithecine hominins, known from several skull and dental fragments dated between 3.5 and 3.0 Ma, about the same age as *Au. deyiremeda* and *Kenyanthropus platyops*; Chad.

Australopithecus deyiremeda a proposed new hominin species, based on a 2015 description of a jaw found in Ethiopia, dated between 3.5 and Ma.

Australopithecus sediba a possible relative of *Homo sapiens* from around 2 Ma, known from two almost complete skeletons found in 2008 near the Malapa Cave, north of Johannesburg, South Africa. A significant find for being possibly the only hominin specimen known between the *Au. afarensis* known as Lucy (about 3.2 Ma) and the *Homo erectus* known as Turkana Boy (about 1.5 Ma). The disputed dates proposed for the more recent discovery *H. naledi* vary between 2.5 and 0.9 Ma.

Austral realm the modern geographic region that includes Australia, New Zealand, New Guinea, and the islands near them; the temperate areas of South America and South Africa; and Antarctica.

Austroptyctodus gardineri See **Gogo Formation**.

Autapomorphy a distinctive derived character possessed uniquely by a particular lineage and not possessed by others in comparison; see also **synapomorphy**.

Autochthonous referring to an assemblage of fossils preserved undisturbed in their life position and location; see also **taphocoenosis**.

Avalofractus an Ediacaran genus of rangeomorphs. It was about 2 inches long, with alternating fernlike fronds branching off from a central stalk. Known only from the Avalon Peninsula, Newfoundland, Canada; 575–560 Ma.

Avalon Assemblage see **Mistaken Point**.

Avemetatarsalia a clade that includes the **Ornithodira** (*q.v.*) and the Aphanosauria (a small clade of gracile reptiles of the Middle Triassic).

Aves a group of winged vertebrates, almost all capable of flight to some degree. Although their origins and line of descent are still debated, the almost unanimous consensus is that birds evolved from feathered dinosaurs. The Enantiornithiformes are the earliest large group of primitive birds, but others are ***Confuciusornis*** (130–125 Ma), ***Enaliornis*** (100–94 Ma), ***Ichthyornis*** (87–82 Ma), and ***Hesperornis*** (84–78 Ma). See also ***Protoavis***.

Avetheropoda a disputed clade that excludes most dinosaurs, including only allosaurids, coelurosaurids, and birds.

Aviculopecten a speciose genus of marine bivalves in the order Pectinida. About 1 inch long, the inarticulate shell has a short, straight hinge with short wings, very fine radial ribs, and some fine concentric ornamentation. Global distribution, Early Devonian to Cretaceous, 390–100 Ma.

Avisauridae a family of euenantiornithean birds, poorly known but possibly closely related to dinosaurs; North and South America and Europe, Early to Late Cretaceous, 110–66 Ma.

Aysheaia a genus of Cambrian soft-bodied animals superficially resembling a caterpillar, one of the enigmatic animals of the burgess shale fauna, possibly related to the modern Onychophora. Its body consisted of 10 segments, each with a pair of appendages. North America and possibly China, early to middle Cambrian.

Azhdarchidae a family of pterosaurs in the suborder Pterodactyloidea. Although several partial specimens may date back to the Early Cretaceous, it is known well only toward the end of the period. The family is known for very large species, including the leading candidates for largest pterosaur, *Quetzalcoatlus* and *Hatzegopteryx*, both of which had wingspans of about 40 feet. But a 2009 discovery of a cat-sized azhdarchoid in British Columbia (between 80 and 70 Ma) shows that some small pterosaurs were still competing with birds at the end of the Cretaceous**.** Global distribution, Early to Late Cretaceous.

B

Background extinction see **extinction.**

Bacteria the major domain of prokaryotes, single-celled organisms without a defined nucleus. They are abundant in every environment from the Mariana Trench to the Himalayas, and there is even some evidence of bacteria on the surface of Mars. On Earth these microbes constitute a greater biomass than all other animals and plants combined. The earliest evidence of bacteria is cyanobacteria-like fossils 3.5 billion years old. See also **Archaea** and **Eukaryota**.

Bactrites a genus of nautiloid cephalopods in the order Bactritida. Generally straight-shelled, it may have been ancestral to the ammonoids and coleoids, and it was also one of the few nautiloids that survived the end-Permian extinction. Global distribution, Early Devonian to Early Triassic.

Bactrosaurus a genus of early neornithischian hadrosaurs. About 20 feet long and estimated at up to 1.5 tons, *Bactrosaurus* was a relatively small duckbill. Incompletely known, it probably had a small crest on its narrow skull and may have had small spines on its back. China, Mongolia, and Tajikistan; Late Cretaceous, probably Campanian.

Baculites "walking stick," an unusual genus of large orthocone ammonoids in the order Ammonitida and superfamily Turrilitoidea. Widespread in the Late Cretaceous, *Baculites* evidently lived in large shoals, although not so numerous as the earlier orthocerid nautiloids that form key Ordovician beds worldwide. It is very similar in appearance to the orthocerids but is differentiated by a relatively simple suture pattern. From 6 inches to 6 feet long and sexually dimorphic, the male baculitids average less than half the size of the females. In cross section, it is oval and often found so because the fossil shell fractures easily. The genus contains many index fossils for the western interior of North America, such as *B. clinolobatus* of the Pierre Shale (69 Ma). Cosmopolitan, Cretaceous.

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Bahariasaurus a genus of large but swift ceratosaurian dinosaurs similar in size to *Tyrannosaurus rex* and *Carcharodontosaurus*. Discovered in 1924 by Ernst Strömer but lost with his other specimens in 1944; see also ***Spinosaurus*** and ***Deltadromeus*****.** North Africa, Late Cretaceous, about 95 Ma.

Balcoracania an unusual genus of redlichiid trilobites in the family Emuellidae. It is less than an inch long, with a semicircular cephalon. Its most striking feature is a high number of thoracic segments (almost 100 in *B. dailyi*), some with pleural spines as long as the two genal spines. Australia and Antarctica, early Cambrian.

Baleen the fringed strips of gristle-like material used by mysticete whales to filter out the small organisms that they eat. It is suspended from the upper jaw in strips between 1 and 11 feet long. Although often called whalebone, baleen is not bony but consists of the hair and nail material keratin. Most of the stem-mysticetes of the Eocene and Oligocene were toothed, and the earliest fossils of baleen are known only from the middle Miocene. Since baleen does not fossilize easily, its earliest appearance is unknown, but see also **Aetiocetidae**.

Balizoma variolaris the type species of the genus, phacopid trilobites in the family Encrinuridae. With strikingly coarse tubercles on the cephalon, it is one of the several "strawberry-headed" genera. Europe and North America, restricted to Silurian.

Baltica the name given to the land mass that is now Northern Europe when it was a separate continent from the Cambrian to the Middle Ordovician.

Baltoniodus triangularis a species of conodonts in the family Balognathidae. Its first appearance marks the beginning of the Middle Ordovician at 470 Ma. China.

Baluchitherium see ***Paraceratherium***.

Bambiraptor feinbergi a possible species of Late Cretaceous dromaeosaurs, related to velociraptors. About 3 feet long and delicately boned, it was bipedal and is notable for its long, winglike arms. *Bambiraptor* is known only from a single complete skeleton found in 1994 at Choteau, Montana, possibly a juvenile. In fact, in the absence of other specimens, it may turn out to be a juvenile specimen of the lightly built dromaeosaur *Saurornitholestes*, which is known from widely scattered locations in Canada and the United States. Late Cretaceous, 75 Ma.

Banffia a genus of primitive animals placed tentatively in the subphylum Vetulicolia. Although it is known from hundreds of specimens from the Burgess Shale, its classification is unsettled. About 4 inches long, its oval body and flat tail are twisted. Canada, middle Cambrian, 508 Ma.

Bangiomorpha pubescens a species of red algae in the order Bangiales. It is the earliest-known complex multicellular organism and also the earliest example of

sexual reproduction, as evidenced by its differential spore and gamete formation. Canada, Mesoproterozoic, 1200 Ma.

Bankia a genus of shipworms, marine bivalve mollusks in the family Teredinidae; global distribution, Early Jurassic to Recent.

Baragwanathia a genus of primitive plants in the order Drepanophycales. The earliest-known lycopod club moss and one of the first vascular plants, it is known best from Australia. Global distribution, late Silurian to Early Devonian.

Barbaturex morrisoni a species of large lacertilian squamates in the suborder Iguania. Known only from dental and skull fragments but considered one of the largest iguanians, it grew up to 6 feet long and was herbivorous. It is the earliest-known representative of the modern clade Acrodonta. Burma, middle to late Eocene.

Barbourofelidae a family of carnivorous mammals in the suborder Feliformia and family Barbourofelidae. Muscular and up to the size of a small lion, the Barbourofelidae were one of the groups known as false saber-toothed cats. They were more primitive and generally smaller than the true felids. North America, Europe, Asia, and Africa; Miocene to Pliocene.

Barnacles see **Cirripedia**.

Barosaurus a genus of very large sauropod dinosaurs in the family Diplodocidae. Resembling its larger cousin *Supersaurus*, it was about 85 feet long, with a long tail and a long and very robust neck. *Barosaurus* is closely related to another diplodocid from Tanzania, *Tornieria africana*. North America and southern Africa, Late Jurassic, 150 Ma.

Barychilina a genus of marine ostracods in the order Metacopida. Its shell was generally oval with fine ridges. Cosmopolitan, Silurian to Carboniferous.

Barylambdidae a small family of pantodont mammals in the extinct order Cimolesta. They were herbivorous and tapir-like, the largest about the size of a small horse. Paleocene to early Eocene.

Baryonyx "heavy claw," a genus of theropod dinosaurs in the family Spinosauridae, very similar to *Suchomimus*. About 25 feet long and weighing more than a ton, it had a large claw on its first finger and a triangular nasal crest. The baryonychines differed from most spinosaurids in having no dorsal fin or sail, and their long, narrow gharial-like snout indicates that they were at least partly fish eaters. England and Iberian Peninsula, Early Cretaceous, 130–125 Ma.

Basilemys variolosa a species of large turtles in the family Nanhsiungchelydidae. Almost 5 feet long, it had a flattened and subrectangular carapace 3 feet wide. It is

probably related to extant Central American turtles. Canada, Late Cretaceous, 77–76 Ma.

Basilosaurus a genus of archaeocete whales in the family Basilosauridae, closely related to the slightly earlier protocetids. Fully aquatic, *Basilosaurus* had a completely flexible backbone for efficient propulsion and by vestigial external hindlimbs too small to be used for swimming. It reached lengths of up to 40–65 feet and was the largest marine animal of the late Eocene. Africa and North America, Eocene.

Bat see **Chiroptera.**

Batesian mimicry the name given to camouflaging structural mimicry used for protection from predation. The mimicking organism (usually uncommon but good-tasting) closely resembles another that predators have learned to avoid because, although abundant, it is foul-tasting, venomous, or stinging. First analyzed and explained by Henry W. Bates in the 1860s, it is observed throughout the plant and animal domain but is most common in invertebrates. A related kind of deception called Müllerian mimicry involves two distasteful or poisonous species that have evolved to resemble each other. A famous example of Müllerian mimicry is the case of *Danaus plexippus* (monarch butterfly) and *Limenitis archippus* (viceroy), which were long thought to be in a Batesian relationship until the viceroy was found to be also unpalatable to predators; research continues, with conflicting reports. Mimicry is difficult to identify in the fossil record because it usually involves surface coloration, scent, or sound.

Bathornithidae a family of birds in the order Cariamiformes, closely related to the Phorusrhacidae and to the extant seriemas. Generally flightless, the family also includes at least one genus capable of flight, *Neocathartes*. North America, middle Eocene to early Miocene.

Bathyuriscus a genus of trilobites in the order Corynexochida and family Dolichometopidae. It was 1.5–2 inches long, had crescent-shaped eyes, and had a well-developed pygidium (reflected in its "deep tail" name). The *Bathyuriscus* Zone is middle to late Cambrian, beginning about 509 Ma.

Batocrinidae a large family of camerate crinoids in the order Monobathrida; known mainly from North America, Devonian to Mississippian.

Batoidea a superorder of elasmobranch fish in the infraclass Euselachii, including the skates, rays, and sawfish. Generally benthic, except for the pelagic manta rays, they are noted for their expanded pectoral fins; these, especially in the skates and rays, resemble wings. The Batoidea offer a good example of convergent evolution when compared with the unrelated rhenanid placoderms (e.g., *Gemündina*), which also had expanded pectoral fins. Global distribution, Early Triassic to Recent.

Batrachia the clade that includes frogs (Anura) and salamanders (Urodela). Global distribution, Early Triassic to Recent.

Baudicrinus a genus of Early Triassic crinoids in the order Encrinida and family Dadocrinidae. Known only from a 2015 find in Oman, it is the earliest definitive encrinid and a possible stem genus of the Articulata. Oman, 251 Ma.

Bauplan a German term sometimes used to refer to the body plan of an organism; for **body plan** see **Ediacaran biota** and **Cambrian**.

Bedding plane a surface of a stratum of rock on which a succeeding stratum is laid down, marking the beginning of the upper layer and the end of the lower.

Beecher's Trilobite Bed a Konservat-Lagerstatten near Rome, New York. It is in a stratum of the deep-ocean Frankfort Shale, dated at about 445 Ma, that contains a remarkable assemblage of about 30 Ordovician animals, many pyritized (replaced by iron sulfide). It is notable for preserving many soft tissue features of trilobites (especially *Cryptolithus*, *Triarthrus*, and larval *Cornuproetus*) and other marine animals. Extensively explored by Charles Beecher in 1893, the site was thoroughly excavated by a large team in 1989. The United States, Late Ordovician.

Beelzebufo a genus of large toads in the extant family Leptodactylidae, related to the Ceratophryidae of South America. Many specimens have been found on Madagascar in strata dated around 70 Ma, after Africa and India had begun to separate from South America, isolating *Beelzebufo* from its ceratophryid cousins. Up to 16 inches long and among the largest of all frogs, it probably bore bony scutes on its head. Madagascar, Late Cretaceous.

Beetles see **Coleoptera**.

Behemotops a genus of herbivorous aquatic or marine mammals in the order Desmostylia. The most basal of the known desmostylians, *Behemotops* is known from around the North Pacific. The United States, Canada, and Japan, early to late Oligocene.

Beipiaosaurus inexpectus a genus of feathered theropod dinosaurs in the superfamily Therizinosauroidea, known from two individuals of about 120 Ma. From 6 to 7 feet long with 4-inch claws and stiff, narrow proto-feathers, it probably did not fly. Although a theropod, it seems to have adapted to a herbivorous diet. *Beipiaosaurus* is one of several feathered dinosaurs in the Jehol biota. China, Early Cretaceous, 120 Ma.

Beishanlong grandis a species of ostrich-shaped dinosaurs in the family Deinocheiridae. One of the largest ornithomimosaurs known, more than 25 feet

long and weighing 1.5 tons, it had digging claws and powerful forelimbs. China, southern Gobi Desert, Early Cretaceous, 110 Ma.

Belantsea a genus of chondrichthyan fish in the family Petalodontidae. It was 2–3 feet long, deep-bodied with large pectoral and ventral fins but a small tail fin, a body plan that suggests it was a slow swimmer. It had a bulbous shape and an unusual petalodont dentition which enabled it to eat crinoids and encrusting organisms like sponges. Montana, Early Carboniferous, about 350 Ma.

Belemnella a genus of belemnites in the order Belemnitida. The species *B. lanceolate* and *B. obtusa* are important in Maastrichtian stratigraphy. Europe, Late Cretaceous, 71–66 Ma.

Belemnitida "dart-shaped," a large order of Mesozoic squid-like cephalopods in the extant subclass Coleoidea and extinct superorder Belemnoidea. The belemnites appeared in the Early Triassic and were widespread in the Jurassic and Early Cretaceous, becoming extinct at the end of the Cretaceous.

Belemnoidea a superorder of mollusks in the extant subclass Coleoidea. They are often referred to as belemnites, a term more precisely referring to the Belemnitida, the principal order in Belemnoidea. The other belemnoid orders are the Aulacocerida and Phragmoteuthida (both Permian to Jurassic) and the small Cretaceous group Diplobelida.

Belemnoids were from 4 to 8 inches long and had ten arms; like other cephalopods, they had an ink sac, beak, tentacles, and large eyes. Unlike other cephalopods, they had a bullet-shaped calcitic internal structure called a rostrum, which was often fossilized. The aragonitic, chambered phragmocone was sometimes also fossilized with the rostrum. All belemnoids became extinct at the end of the Cretaceous but are closely related to modern cuttlefish and more distantly to the Decapodiformes in general.

Bellerophon an enigmatic genus of marine gastropod mollusks, traditionally considered a gastropod. The shell is rounded and symmetrically coiled, 3–4 inches long, with a broad aperture. See **bellerophontomorphs**. Global distribution**,** Silurian to Triassic.

Bellerophontomorphs a large and enigmatic group of marine gastropod mollusks, formerly placed in the paraphyletic order Archaeogastropoda. Generally coiled symmetrically and up to 4 inches long, the group includes a variety of shapes (notably *Bucanopsis* and *Plectonotus*) that have invited reclassification. Some recent research places them in such groups as the Monoplacophora, the Helcionelloida, or a new class Bellerophonta or Tergomya, with no consensus reached. Global distribution, Early Cambrian to Triassic.

Bellinurus a genus of freshwater arthropods in the order Xiphosurida. Though less than 2 inches long, *Bellinurus* is related to modern horseshoe crabs (see ***Limulus***). Europe, Devonian to Carboniferous.

Beltanelliformis a problematic genus of fossils, probably of cyanobacterial origin. Known only from isolated discoidal impressions, it was first assigned to the cnidarian order Actiniaria but is now considered a cyanobacterial colony and tentatively assigned to the Ediacaran biota. Russia and possibly Canada, China, Australia, and Europe; late Ediacaran, 575–541 Ma.

Bennettitales a group of small cycad-like trees whose classification is disputed. They were seed-bearing and about 7 feet high. Although their leaves resemble cycads, they are considered a separate monophyletic group, divided into two families, the Williamsoniaceae and the Cycadeoidaceae. Widespread Triassic to Cretaceous and surviving sparsely to the Oligocene.

Benthic living at the lowest level of a body of water, from eulittoral to abyssal, as opposed to living in the water column. The benthos includes organisms living on the surface of the seafloor and also in the sediment (see **epifaunal**). The term generally refers to oceans but may also be used for lakes and rivers. See also **nektic** and **nektobenthic**.

Benthosuchus a genus of stereospondyl amphibians, variously placed in the superfamilies Trematosauroidea and Capitosauroidea. About 5 feet long and slender, it is known only from Russia. Early Triassic, 250 Ma.

Bernissartia a genus of small, semiaquatic crocodylomorphs in the family Bernissartiidae. Similar to modern crocodiles, it is considered a neosuchian. Named for specimens found at the Bernissart mine in Belgium, it was less than 3 feet long, and its dentition was adapted to crushing shellfish and crustaceans but also to catching fish. North America and Europe, Early Cretaceous, 135–125 Ma.

Bernissart site a Belgian coal mine where many important fossils have been found. It is especially important for the specimens of *Iguanodon* found there in the 1870s. Early Cretaceous, 135–125 Ma.

Berriasella jacobi a species of ammonoids whose first appearance marks the beginning of the Early Cretaceous at 145.0 Ma; Europe.

Bertie Waterline name given to several upper Silurian deposits in New York that contain well-preserved arthropod and plant fossils, known especially for *Eurypterus remipes*; the United States, late Silurian.

Bethia serraticulma a species of brachiopods placed variously in the rhynchonellate order Orthida or the strophomenate order Strophomenida, known only from one specimen found in a carbonate nodule (see **Herefordshire Nodules**). Digital reconstructions of *Bethia* show excellent soft-part morphology. England, Silurian.

Beyrichicopina a large suborder of ostracods in the order Palaeocopida; North America and Europe, Ordovician to Early Mississippian.

Biarmosuchia a suborder of basal therapsids, including *Biarmosuchus* and *Eotitanosuchus*. They were generally similar to sphenacodonts, with long canine teeth. Russia, middle to late Permian.

Bighorn Basin an arid area in northern Wyoming that is an important study site for the transition from Paleocene to Eocene. About 10,000 square kilometers in area, it is notable for the plant life and the large numbers of mammal species recorded in its varied strata.

Bilateralism having a definite and symmetrical left and right side, as opposed to amorphous animals like sponges and jellyfish.

Bilaterians the bilaterally symmetrical animals, excluding sponges, cnidarians, placozoans, and ctenophores. They display bilateral symmetry and have an anterior-posterior body orientation. The earliest-known specimen may be microfossil embryos from an Ediacaran deposit in China (see ***Vernanimalcula guizhouena***), thought to be 580 million years old; these are also the earliest-known embryos of complex animals. Ediacaran to Recent.

Billingsellida an order of articulate brachiopods in the class Strophomenata, among the first and most primitive articulate brachiopods. Middle Cambrian to Middle Ordovician.

Bilobites see ***Dicoelosia***.

Biocoenosis an assemblage of organisms living together at one time, an ecological community.

Biochron a period of time represented by a relatively small biostratigraphic zone, one characterized by a particular fauna or flora.

Biosphere 1. the area favorable for the existence of living organisms, including the lithosphere, hydrosphere, and atmosphere. 2. All the living organisms of the Earth and its atmosphere.

Biostratigraphy the science of correlating geographically separated rock strata by identifying the biotic content and time relations of the strata. It is based on faunal succession, the process in which species change over time.

Biostratinomy a subsection of taphonomy, dealing with the orientation of the remains of an organism and what it says of the processes the organism experienced between its death and its burial, such as transportation and chemical change.

Biota the total fauna and flora living or preserved as fossils within a certain area or period of time.

Biozone a stratigraphic unit of specific geological strata defined by various combinations of taxa present in the strata.

Bird-hipped dinosaur a general term referring to the ornithischian dinosaurs.

Birds see **Aves.**

Birgeria americana a species of large predatory fish in the family Birgeriidae, known from a partial skull described in 2017. A bony fish about 7 feet long, it lived in water warmer than previously thought possible for the development of eggs. Nevada, United States, Early Triassic, 251 Ma.

Birkenia a genus of early agnathan fish in the family Birkeniidae. From 3 to 4 inches long and toothless, it had a terminal mouth, lateral eyes, scales, a series of stout dorsal spines, and a reversed heterocercal tail. Northern Europe and Canada, Silurian to early Devonian.

Bison latifrons a species of giant bison in the family Bovidae, possibly the largest bovid known. It weighed more than a ton, stood 8 feet high at the shoulder, and had forward-pointing horns 7 feet wide. North America, Pleistocene to Recent, becoming extinct about 22,000 years ago.

Bison priscus a species of large-horned bison in the family Bovidae. Its extinction in the late Pleistocene was probably related to human activity. North America, Pleistocene to Recent.

Biston betularia the peppered moth, an extant species of lepidopterans in the family Geometridae, a family dating back to the Eocene. Two forms of *Biston* (*B. b. form typica* and *B. b. f. carbonaria*) have evolved in the Holocene and have been studied in detail since the 1850s. Their variation in color over two centuries, caused by industrial melanism, results in differential predation by birds and is now generally accepted as a clear example of Darwinian natural selection in action. Cosmopolitan, Recent.

Bitheca a smaller theca that appears in many graptolites, growing alternately on both sides of the autothecae.

Bithecocamara an enigmatic genus of pterobranch encrusting graptolites in the order Camaroidea, the only camaroid with bithecae; Baltic, Ordovician.

Bivalvia mollusks that typically have shells with two hinged valves, formerly called Pelecypoda. Including mainly clams, mussels, and oysters, they are not related to the two-valved brachiopods, which are different organisms that have developed a similar shell because of a similar lifestyle, an example of convergent evolution. The two valves of a bivalve are usually symmetrical, but there are several exceptions. The rudists, for example, are horn- or tube-shaped bivalves whose external morphology seems to bear no similarity to other bivalves. And shipworms (see ***Bankia*** and ***Teredo***) have only a pair of very small shells, at the anterior end of a tubelike body, with which they bore through wood. The two valves are generally held together by a ligament, but many bivalves also have interlocking teeth on both sides of the hinge; the number and arrangement of the teeth are important in classifying them. Global distribution, early Cambrian to Recent.

Bjuvia a genus of short trees with a crown of broad lanceolate leaves atop a squat, branchless trunk; Europe, Early Triassic.

Blackberry Hill a Lagerstätte in Wisconsin consisting of several quarries. It is best known for its extensive trace fossils, mostly trackways left in a shallow-water sandstone formation. Also notable are body fossils of a phyllocarid and a euthycarcinoid (for the latter, see ***Mosineia***), considered by some to be the earliest body fossils of an animal walking on land. The United States, middle or late Cambrian.

Blastoidea a class of Paleozoic sessile pelmatozoan echinoderms in the subphylum Blastozoa. Up to 1 inch wide, they are sometimes called sea buds because of their nutlike shape. Commonly stacked, they were attached to the sea floor on a stem. The two blastoid orders are Fissiculata and Spiraculata. Global distribution, Ordovician to late Permian.

Blattodea the order of insects that includes cockroaches and termites; synonym Blattoptera. The ancestors of cockroaches are known from the Late Carboniferous, and modern roaches appeared in the Triassic. Termites probably evolved in the Permian or even the Late Carboniferous, but specimens are known only as far back as the Early Cretaceous.

Blikanasaurus a proposed genus of sauropodomorph dinosaurs, known only from one limb bone; South Africa, Late Triassic, 210–202 Ma.

Bobasatraniidae a small family of deep-bodied chondrostean fish, in the crown group of the Actinopterygii. They are characterized by a diamond-shaped body; a

forked tail fin; and long, thin pectoral fins. North America, Europe, and Africa; late Permian to Early Triassic.

Bobcaygeon Formation an Upper Ordovician rock formation in the Lake Simcoe region of Ontario, overlain by the Verulam Formation. Several locations here contain exceptionally preserved fossils, especially of early crinoids that had evolved as part of the Great Ordovician Biodiversification Event of the Early and Middle Ordovician. From a quarry near Brechin that is sometimes described as a Konservat-Lagerstatten, a new genus of dicyclic camerate crinoids, *Priscillacrinus*, and several new species of *Reteocrinus*, *Archaeocrinus*, and *Cleiocrinus* were described in 2018. Canada, Late Ordovician.

Body fossil see **fossil.**

Body plan see **Bauplan, Ediacaran biota,** and **Cambrian**.

Bolca deposits a small Eocene Konservat-Lagerstatten in northern Italy, dated at 50–49 Ma. Of several fossiliferous sites in the area of Bolca, the principal ones, the Pesciara and Monte Postale, have produced a great number of very well-preserved fish and other fossils from near the end of the Ypresian. Slightly older than the Messel Shale deposits, Bolca represents a time of very warm temperatures and high carbon dioxide levels in the atmosphere. Italy, early Eocene.

Bone bed a fossil site that contains a large number of animal macrofossils. Of special importance are bone beds where many animals died abruptly, leaving whole-body fossils. Those where whole-body fossils of many different species are found together raise questions about the cause of the deaths, from flash floods to accumulations of poisonous substances. The Messel Shale Pit, for instance, contains many different types of animals, including birds and bats, and also turtles that died in the act of copulating; poisonous gases have been the most common cause suggested. Toxic algae have been proposed as a possible cause of the deaths of several layers of fossils in the Maevarano site in Madagascar. No conclusive evidence has been found in either case.

Bony fish see **Osteichthyes.**

Bootherium nivicolens a species of musk ox in North America whose extinction in the late Pleistocene may have been caused by humans.

Borealopelta *markmitchelli*: a genus of ankylosaurian dinosaurs in the family Nodosauridae, known from a whole-body specimen described in 2017. Recovered from an oil sand mine in central Alberta, it is the best-preserved specimen known of an ankylosaur. About 30 feet long, the specimen has soft tissue as well as its armor (many sharp-pointed osteoderms and two long shoulder spines) in life position. Like other nodosaurids, it had no club at the end of the tail. The keratin in the skin

and scales indicates countershading, with a dark reddish-brown dorsal coloration and a lighter underside. Canada, Early Cretaceous, 110 Ma.

Borealosuchus a genus of crocodilians widespread in North America from the Late Cretaceous up to the middle Eocene. About 9 feet long, it is one of several genera of crocodilians that survived the end-Cretaceous extinction.

Borophaginae a large subfamily of canids that flourished in North America as the Hesperocyoninae declined in the Oligocene. Notable for a powerful, bone-crushing bite and a small fifth toe on the rear feet, more than 60 genera of borophagines such as *Borophagus* and *Tomarctus* dominated the continent from the sub-Arctic to Panama throughout the Miocene. The fox-sized *Archaeocyon* is the earliest known, and the largest grew to the size of a bear, up to 5 feet long. Early Oligocene to late Pliocene.

Boskovice Furrow a large site in Moravia that contains a series of deposits in upper Carboniferous and lower Permian strata. It is important for tetrapods from the Permian strata, especially in the family **Discosauriscidae**, *q.v.* Czech Republic.

Bostrychoceras a genus of heteromorph ammonoids in the order Ammonitida and family Nostoceratidae. Loosely coiled but slightly tighter than in its cousin *Nostoceras*, its shell is covered with fine, dense ribs and forms a long, slightly open helical spire. Europe, Africa, and North America; known only from the Campanian Age near the end of the Cretaceous.

Bothriocidaris a genus of echinoids in the family Bothriocidaridae. Globular and covered with spines and tube feet, it is known only from Upper Ordovician deposits in Estonia, Scotland, and North America.

Bothriolepis a genus of heavily armored placoderm fish in the order Antiarchi. Generally 1 foot long, with some more than 3 feet, *Bothriolepis* had a slender and somewhat flattened head and body and was especially notable for a pair of long, jointed, spine-like pectoral fins with small spines on them. Its closely spaced eyes were located on the top of the headshield, along with a light-receptive pineal eye, and its mouth was on the underside. It had heavy anterior armor but no posterior armor, not even scales. Bottom-dwelling and mainly freshwater rather than marine, it may have been able to use its pectoral fins to move across mud flats into freshwater ponds. Widespread, abundant, and diverse in the Middle to Late Devonian, it became extinct with all other placoderms at the end of the Devonian.

Botryococcus an extant genus of one-celled freshwater algae that can also grow in brackish water environments. It is notable for a high hydrocarbon content in and outside its thick, waxy cell walls, held together by a lipid biofilm, and is useful in interpreting paleoenvironments. Triassic to Recent.

Bourgueticrinida an order of stalked articulate crinoids. Cosmopolitan, Triassic to Recent.

Bovidae a family of horned, cloven-hoofed, ruminant mammals in the order Artiodactyla, including cattle, sheep, bison, goats, buffaloes, and antelopes. The largest artiodactyl family, they are distinguished from the Cervidae by their hollow, non-deciduous, unbranched horns; all male bovids and two-thirds of the females have two or more horns. The earliest-known bovid is *Eotragus*, which appeared in Eurasia around 20 Ma. Global distribution, early Miocene to Recent.

Bowfin see ***Amia calva***.

Bowman site a bone bed found near Bowman, North Dakota, and described in 2019; also called "Tanis site." Part of the Hell Creek Formation and dated at 66 Ma, it may represent fossil deposition caused by a series of tsunami-like seiches in a previously unknown arm of the Western Interior Seaway. The fossil content and manner of deposition suggest that the site may have resulted from secondary seismic waves caused by the impact of the Chicxulub asteroid in the Gulf of Mexico. The unusual bone bed is a 4-foot-thick deposit overlain by a layer with iridium content similar to that associated with the Chicxulub impact. It purportedly contains three-dimensional articulated specimens, buried haphazardly alongside detritus that might have come from an onshore wave surge. The site seems chaotic, with fragments of marine fossils such as ammonoids juxtaposed with articulated bodies of continental fish including paddlefish and sturgeon. The gill rakers of many of the fish contain spherules similar to those found elsewhere that are associated with the Chicxulub impact. Since the site has been only superficially described, its significance is still unclear. The United States, Late Cretaceous, 66 Ma.

Brachiopoda "arm foot," a phylum of solitary marine invertebrates characterized by a dorsal (brachial) and a ventral (pedicle) valve; a pedicle, a muscular extension of the body wall used by most genera to attach to the substrate; and an internal lophophore, which is bilobate and typically horseshoe-shaped but often in long loops. In some articulate brachiopods, the two lobes of the lophophore are supported by calcareous support structures called brachidia, which are attached to the brachial valve (see **Spiriferida**).

The currently accepted classification system recognizes three subphyla: Rhynchonelliformea (more than 4500 genera), Linguliformea (more than 240 genera), and Craniiformea (about 40 genera). Appearing later than most other animal phyla, brachiopods arose in the Tommotian of the early Cambrian. They quickly became one of the most common animals, however, very widespread from the Ordovician to the Devonian. Several classes declined in the late Paleozoic, and only one-third of brachiopod genera survived the end-Permian extinction. Although the bivalve mollusks have become dominant, brachiopods have continued to increase slightly in number in the Cenozoic, with about 250 species of brachiopods still

extant, the most famous being *Lingula*, which has remained essentially unchanged in shape since the Cambrian. Five classes are now extinct: Paterinata, Chileata, Obolellata, Kutorginata, and Strophomenata. Six orders are extant: Lingulida, Craniida, Rhynchonellida, Terebratulida, Thecideida, and Acrotretida. The rhynchonellate terebratulides are the most common living brachiopods.

Called lampshells, brachiopods are superficially similar to bivalves but are not mollusks. The two-halves of their shells are not mirror images of each other, as in bivalves, whose plane of symmetry runs between the valves; in brachiopods the plane of symmetry runs through the valves. The internal body parts are relatively sparse compared to those of the bivalves. Most fossil brachiopods are 1–3 inches wide, and the largest known is 9 inches wide. See also **punctate**.

Several genera were epi-planktic and a few were nektic, swimming in the style of scallops. Extinct brachiopods are significant index fossils in the Paleozoic because of their broad distribution and their abundance and diversity at several taxonomic levels, especially for the Devonian and Carboniferous. While almost all fossil brachiopods lived in relatively shallow water, some of the extant ones have moved into deep water. Cambrian to Recent.

Brachiosaurus a genus of titanosaurian sauropodomorph dinosaurs in the family Brachiosauridae. Estimated at 85 feet long and 32 tons, it is one of the largest sauropods. Its forelimbs are relatively elongated, and its neck is very long, but its tail is short for a sauropod. The United States, Europe, and Africa; Jurassic.

Brachyaspidion a genus of small trilobites in the order Ptychopariida. *B. microps* (1 cm) and *B. sulcatum* (4 cm) are among the dozens of trilobites in the Wheeler Shale Lagerstätte. North America, middle Cambrian.

Brachyceratops an obscure genus of ceratopsian dinosaurs, known only from partial juvenile specimens found in Campanian strata in Montana and Alberta; North America, Late Cretaceous.

Brachydont dentition low-crowned teeth with long, narrow roots. They do not grow throughout life in all animals but do in some, such as rodents.

Brachylophosaurus a genus of hadrosaurid ornithischian dinosaurs in the subfamily Saurolophinae. The type species is *B. canadensis*, but the genus is known from many skeletons and casts showing soft tissue detail, including tendons and hundreds of thin tracks that have been interpreted as evidence of stomach parasites. Montana and Alberta, Late Cretaceous, 80–75 Ma.

Brachyopterus an early eurypterid in the suborder Stylonurina and family Rhenopteridae. It was small but robust, with five pairs of walking legs and a short telson. Known only from Wales, Middle Ordovician, 460 Ma.

Brachysaurus see ***Prognathodon***.

Brachythoraci the largest suborder of armored arthrodires. The early Brachythoraci were relatively small, like the agnathans, but the best known was the gigantic *Dunkleosteus*, which grew to 30 feet long. Like all other placoderms, they became extinct at the end of the Devonian. Global distribution, Early to Late Devonian.

Brachytrachelopan mesai a species of relatively small sauropod dinosaurs in the family Dicraeosauridae. Known from one partially articulated skeleton, *B. mesai* was about 35 feet long and is notable for its short neck, which is shorter than that of any other sauropod. Argentina, late Triassic.

Bradgatia a monospecific genus of Ediacaran fossils, possibly a rangeomorph. Dated at about 570 Ma, *B. linfordensis* is a small, bush-like petalage, a cluster of 6–8 petals a few inches high. Found especially in the Ediacaran assemblages at Mistaken Point and Charnwood Forest; Canada and England, Ediacaran.

Bradoriida a stem group of basal crustaceans widespread in the early Paleozoic; formerly considered ostracods and called Archaeocopida. Small, with a thin, bivalved carapace over the head and body, they had a shell with high-chitin content, only slightly calcified. Global distribution, early Cambrian to middle Ordovician.

Bradyodont having paired hard, enameled toothplates in the upper and lower jaw, used to crush prey. Several groups of fish that flourished in the Carboniferous with this dentition are sometimes referred to as Bradyodonti. Late Devonian to Permian.

Brahmapithecus see ***Sivapithecus***.

Branchial referring to gills.

Branchiopoda "gill foot," an extant class of small, segmented crustaceans. Branchiopods have a long but incomplete fossil record, and they may be more closely related to insects than to other crustaceans. Now found mainly in freshwater environments, they are thought to have originated in a marine environment but to have adapted to freshwater because of competition. The class includes several living groups: the Anostraca (fairy shrimp), which are as long as 7 inches; Notostraca (tadpole shrimp); Cladocera; and Laevicaudata, Spinicaudata, and Cyclestherida. The last three (called clam shrimp) generally have chitin shells and were traditionally named Conchostraca. The Lipostraca are known only from the Devonian *Lepidocaris rhyniensis*; the only other extinct order is the Kazacharthra. Global distribution, Late Cambrian to Recent.

Branchiosauridae a family of temnospondyl amphibians in the superfamily Dissorophoidea. Europe and the United States, Late Carboniferous to Early Triassic.

Branchiostegal having covered gills.

Branchiostomiformes see **Cephalochordata.**

Brasilitherium riograndensis a species of small cynodont therapsids in the clade Probainognathia and family Brasilodontidae. Known from a skull almost an inch long that reveals transitional features between cynodonts and early mammals, especially in the nasal cavity. Research in 2018 indicates the presence of a form of the muscle tensor veli palatini, a characteristic of mammals that enables them to suckle their young; this muscle is not known in less advanced cynodonts, such as the well-known *Thrinaxodon* (Middle Triassic). *Brasilitherium* is dated in the Norian, between 227 and 209 Ma. Southern Brazil, Late Triassic.

Brasilodon a genus of small cynodont therapsids in the clade Probainognathia and family Brasilodontidae. Known from several specimens, it was about 5 inches long, and its 1-inch skull is slightly larger than that of its close relative *Brasilitherium*. It has several features that seem to be transitional between advanced cynodonts and early mammals, in dentition, palate, and possibly hearing. *Brasilodon* is known from the same location in Southern Brazil as *Brasilitherium*. Late Triassic, between 227 and 209 Ma.

Bridetherium a monospecific genus of morganucodont mammals. *B. dorisae* is known from a few molariform teeth found with other unidentified morganucodontan teeth in a quarry in Wales. Early Jurassic, 201–190 Ma.

Broiliana a genus of small European mammals, considered a possible ancestor of the family Procyonidae, which became widespread in the Americas in the Miocene. It is known as two species, *B. dehmi* and *B. nobilis*, from Germany and France, respectively. Early to middle Miocene, 23–14 Ma.

Brontosaurus a contentious genus of sauropod dinosaurs. Long considered a junior synonym of *Apatosaurus*, *Brontosaurus* is now thought by some to be a separate genus. For description, see ***Apatosaurus***.

Brontoscorpio anglicus an early species of chelicerates in the class Arachnida and order Scorpiones. Possibly the largest true scorpion, *Brontoscorpio* is dated between 421 and 419 Ma. Known from only a partial pedipalp, it is estimated to have been 3 feet long. See also ***Pulmonoscorpius***. England, late Silurian.

Brontotheriidae "thunder animal," a large family of herbivorous perissodactyl mammals; synonym Titanotheriidae. A sister group to the Equidae in the suborder Hippomorpha, the brontotheres were almost elephant-sized, ranging in height from 2 to 9 feet. They are marked especially by a variety of bony frontal horns, even with a pair of blunt nasal horns in *Megacerops*. Although similar in appearance to rhinoceroses, they are more closely related to horses. The earliest brontothere, the

dog-sized *Eotitanops*, appeared in the early Eocene. North America, Europe, and Asia; early to late Eocene.

Bryophytes "moss plant," a common name for the group of primitive land plants that includes the mosses (clade Bryophyta), hornworts (clade Anthocerotophyta), and liverworts (clade Marchantiophyta). Not vascular and lacking true roots, stems, and leaves, the bryophytes reproduce by spores. Molecular phylogenetic research indicates that the bryophytes were the earliest land plants, probably appearing in the Ediacaran. The earliest definitive bryophytic fossils (such as *Sporogonites*) are dated Early Devonian. See also ***Protosalvinia***.

Bryozoa "moss animals," an extant phylum of small colonial animals that secrete calcified skeletons around the individual zooids' bodies, a process seen also in reef-building corals. Bryozoa is the only phylum of animals that are wholly colonial and also the only phylum with an extensive fossil record to have arisen later than the Cambrian; the earliest-known bryozoan fossils date from the Early Ordovician. Bryozoans are one of the dominant groups of Paleozoic fossils, with tens of thousands of named species, almost all marine. Only a few families survived the end-Permian extinction, but there are still about 6000 living species.

Bubalus cebuensis an extinct species of dwarf water buffalo, less than 3 feet high and weighing about 350 pounds. Descended from much larger buffalo, they experienced island dwarfism when stranded on the small Philippine island of Cebu by a rising sea level between 100,000 and 20,000 years ago. See also ***B. mindorensis***.

Bubalus mindorensis the tamaraw, an extant species of dwarf water buffalo found on the Philippine island of Mindoro. An example of island dwarfism, it descended from larger buffalo stranded on the island by rising sea levels about 20,000 years ago.

Bucanopsis an enigmatic genus of mollusks traditionally placed in the order Bellerophontida and considered a gastropod. Its broad, shelflike lip and other features have led to other classification possibilities. Cosmopolitan, Ordovician to Permian.

Buchia a genus of edentulous bivalves in the superfamily Buchioidea. It has a slender shape, with the left valve larger than the right valve. Known around the Pacific Rim, Jurassic to Cretaceous.

Buenellus a genus of redlichiid trilobites in the suborder Olenellina and family Nevadiidae. It was about 2 inches long, with a semicircular carapace and a slightly vaulted glabella. The best-known species is *B. higginsi*, well-described from the Sirius Passet Lagerstätte; a new species, *B. chilhoweensis*, was described in 2018 from specimens found in Tennessee. North America, early Cambrian, 523–517 Ma.

Bumastus a genus of large (up to 6 inches) trilobites in the order Corynexochida and family Styginidae. *Bumastus* is notable for a smooth, rounded, isopygous exoskeleton without longitudinal segmentation. It had ten narrow thoracic segments and well-developed compound eyes. Global distribution, Early Ordovician to late Silurian.

Bunodont dentition low-crowned, conical or rounded teeth with ridged cusps. Bunodont teeth are separate, often quadrate in shape, and are typical especially of early artiodactyl and suiform mammals.

Bunopithecus a monospecific genus of apes in the gibbon family Hylobatidae. Originally including also *Hoolock*, the genus now is restricted to *B. sericus*. China, known only from the middle Pleistocene.

Bunostegos a genus of reptiles in the suborder Procolophonia and family Pareiasauridae. About the size of a cow, *Bunostegos* was one of the earliest reptiles with somewhat erect posture, holding its legs almost directly under its body. It is known from several skulls and skeletal remains. Niger, late Permian.

Burgess Shale name given to one of the most important Konservat-Lagerstatten, a calcareous black shale formation dated at 508 Ma. The first site, discovered in 1909 by Charles D. Walcott, is located in Yoho National Park, near Kicking Horse Pass in the Rocky Mountains of eastern British Columbia; a second prolific site has been investigated since 2012 in Kootenay National Park (see **Marble Canyon**). The Burgess Shale fauna includes a surprisingly well-preserved assemblage of soft-bodied animals from the middle Cambrian. The fossils are generally allochthonous, probably having been removed from their living location by a series of mudslides. The assemblage evidently represents a complete marine community that includes both nektic and benthic animals. The great diversity and excellent preservation of these very unusual fossils provides a rare view of this period of rapid diversification of animal species. Several specimens are the only known representatives of phyla that are unlike any modern phyla. See also **Chengjiang biota.** Canada, middle Cambrian.

Buriolestes a monospecific genus of sauropodomorph dinosaurs described in 2016. *B. schultzi* was carnivorous, and its length is estimated at 4–8 feet. The specimen (which includes the skull, a forelimb, a hindlimb, and vertebrae) was found near a partial skeleton of the lagerpetid dinosauromorph *Ixalerpeton*.

Santa Maria Formation, Brazil; early Carnian of the Late Triassic, 237–234 Ma.

Butterflies see **Lepidoptera**.

Byssonychia see ***Ambonychia***.

Byssus a bundle of tough, hairlike filaments commonly used by bivalve mollusks to attach themselves to objects, usually rocks or other hard substrate but sometimes, as with *Modiolus*, to detritus in sediment.

Bystrowiella schumanni a species of chroniosuchian reptiliomorphs in the family Bystrowianidae. Known only from fragmentary remains, it may be important in tetrapod evolution. Germany, Middle Triassic, 240 Ma.

C

Cadoceras a genus of ammonoids in the order Ammonitida and family Cardioceratidae. Generally about 4 inches in diameter and 2 inches wide at the aperture, it was involute and sub-globular. Holarctic distribution, Middle Jurassic.

Caecilians a group of legless amphibians in the clade Gymnophiona; synonym apodans. Almost blind, they burrow in wet soil or in the substrate of streams in the tropics worldwide. They have a sparse fossil record, going back at least to the Early Jurassic. See ***Eocaecilia***. Global but mainly tropical distribution.

Caelestiventus hanseni an unusual species of non-pterodactyloid pterosaurs in the family Dimorphodontidae, one of the few desert-dwelling pterosaurs known. Found in an arid area of Utah that was desert in the Triassic, it is known from a complete skull and mandible, and one finger bone. *Caelestiventus* had an unusual dentition and a relatively large estimated wingspan of 5 feet. It had more than 100 multi-cusped teeth, with several long, fang-like teeth at the front of the snout. United States, Late Triassic, 208 Ma.

Caelifera the grasshoppers and locusts, a suborder of chewing herbivorous insects in the order Orthoptera. Caeliferans are mostly ground-dwelling and stridulatory, with strong hind legs and wings. Global distribution, Early Triassic to Recent.

Caenagnathidae a family of maniraptoran theropod dinosaurs, coelurosaurians closely related to the **Oviraptoridae**, *q.v.* Eurasia and North America, Late Cretaceous, 100–66 Ma.

Caenolestidae a family of small South American marsupials in the order Paucituberculata. Commonly called shrew opossums and rat opossums, they were once abundant but are now confined to small areas in the Andes Mountains. Late Oligocene to Recent.

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Caihong juji a species of paravian theropod dinosaurs thought to have had iridescent feathers. About the size of a small duck and bipedal, it weighed about a pound. A prominent lacrimal crest resembles that found in some earlier dinosaurs but not in closely related theropods like *Anchiornis*. It had short forelimbs, a long and narrow skull, and feathers on all parts of the body. Melanosomes on the feathers indicate that those on the head and possibly other areas were iridescent. Yanliao biota, China, Middle Jurassic, 161 Ma.

Cainotheriidae a family of small, herbivorous artiodactyl mammals in the suborder Tylopoda and extinct superfamily Anoplotheroidea. Recognized by a rabbitlike, strongly curved back, they resembled modern hares and rabbits but are unrelated. They diversified rapidly in the Eocene, with only a few persisting into the Oligocene, but then diversified again before disappearing by the end of the period. Europe, Eocene to Oligocene.

Calamistrum a row of fine bristles on the hindlimbs of cribellate spiders, used to comb out the silk threads produced by the cribellum.

Calamitales an order of arborescent sphenopsid plants. Resembling giant horsetails, they were reedlike plants with horizontal rhizomes and segmented and grooved stems, growing up to 100 feet high and 12 inches in diameter. Global distribution, Late Devonian to Permian.

Calamopityaceae a large family of Early Carboniferous gymnosperms in the division Pteridospermatophyta and order Calamophytales. Like *Lyginopteris*, they were small, vinelike trees. North America and Europe, Early to Middle Carboniferous.

Calamophyton a genus of cladoxylopsid plants in the order Pseudosporochnales, growing about 2 feet high and topped with a dense club of short branches. Europe and North America, Middle Devonian.

Calcarea a class of small marine sponges. The only sponges with spicules of calcium carbonate, they are found mainly in shallow tropical waters but have been found as deep as 4000 feet. Three subclasses: the extant Calcaronea and Calcinea and the extinct Heteractinida. Global distribution, early Cambrian to Recent.

Calcaronea an extant subclass of sponges in the class Calcarea, with three- or four-rayed spicules. They may have appeared as early as the Cambrian, were especially prominent in the Cretaceous, and still exist worldwide.

Calceola a genus of solitary rugose corals in the family Goniophyllidae. Known as slipper coral because of its calceolate shape, *Calceola* was semicircular and rested on the seafloor with its flattened convex side down. Global distribution, Early to Middle Devonian.

Calcinea an extant, probably paraphyletic subclass of sponges in the class Calcarea. They have a generally spreading habit, usually yellow or red, with regular three- or four-rayed spicules. Global distribution, Permian to Recent.

Calclamna a genus of sea cucumbers, echinozoans in the class Holothuroidea and extinct family Calclamnidae; Europe and Asia, Early Triassic to Cretaceous.

Callavia a monospecific genus of redlichiid trilobites in the suborder Olenellina; its placement is disputed, but it is one of the earliest trilobites. *C. bröggeri* was oval-shaped and had a semicircular cephalon, a long and narrow glabella, crescent-shaped eyes, a spinose thorax, and a small pygidium. North America, early Cambrian, 530–524 Ma.

Callistophytales an order of vinelike plants in the division Pteridospermatophyta, widespread in the late Paleozoic. North America, Europe, and Asia; Carboniferous to Permian.

Callograptus salteri a species of irregularly branching graptolites in the order Dendroidea. It grew as a fine net of branches with many small thecae. Europe, Asia, and North America; late Cambrian to Early Carboniferous.

Calsoyasuchus see ***Goniopholis***.

Calymene a genus of phacopid trilobites in the family Calymenidae. Some well-preserved specimens of *Calymene* and its relative *Flexicalymene* show appendages and soft body parts. Specimens are frequently found enrolled, rolled into a ball in the manner of the modern terrestrial isopods. From 1.5 to 3 inches long, *Calymene* had a vaulted glabella, two robust cephalic spines, prominent thoracic ribbing, and a short semicircular pygidium. Global distribution, Ordovician to Middle Devonian.

Calyx primarily, the central cup-shaped body of crinoids, resting on a stem, with arms extending outward and upward. In corals, the calyx is a cup enclosing an individual polyp. Also, the cup formed by the sepals of a flower.

Camarasaurus a genus of very large herbivorous dinosaurs, the most common sauropods of North America in the Late Jurassic. The largest species was about 75 feet long and weighed about 52 tons, with a relatively short neck. *Camarasaurus* is named for the weight-saving hollows and air sacs in the vertebrae that were connected to the lungs. Many specimens have been found in the Morrison Formation, some well-preserved, and many exposed in the relieved quarry wall at Dinosaur National Monument. North America, Europe, and Africa; Late Jurassic to Early Cretaceous.

Camaroidea an order of sessile encrusting graptolites known mainly from the Ordovician of the Baltic Sea area. They are distinguished by thecae with a balloon-shaped base and vertical chimney; the best-known genus is *Bithecocamara*. Baltic and Siberia, late Cambrian to Early Ordovician.

Cambaytherium a genus of early placental mammals in the family Cambaytheriidae, formerly placed in the Anthracobunidae; now considered a basal perissodactyl. It is known from several fragmentary specimens found in strata dated 54.5 Ma, when the Indian island continent was nearing Asia after splitting off from Gondwana. The size of a small pig, it has five digits and seems close to the ancestry of horses, rhinoceroses, and tapirs. Its discovery has led to the conclusion that perissodactyls evolved in Asia and spread to North America during the Eocene. Gujarat, India, early Eocene.

Cambrian the first period of the Paleozoic Era, 541–485 Ma. Its macrofossil record is primarily marine, with just a few traces of early terrestrial invertebrates. The marine environment was dominated at first by reef-building Archaeocyatha and other small animals and then increasingly by primitive deuterostomes. Some of the basic animal body plans seem to have appeared in the Ediacaran, but most are first known from early in the Cambrian, probably between 535 and 530. These early species diverged morphologically in a short period of time in what is known as the Cambrian explosion, a sudden radiation of metazoan phyla. The first primitive marine vertebrates (see ***Myllokunmingia, Haikouichthys,*** and ***Zhongjianichthys***) appeared near the end of this brief time.

Camelidae an extant family of even-toed ungulates in the suborder Tylopoda. The first camelids (see ***Protylopus***) appeared in North America about 45 Ma and evolved into several distinct genera, especially in the late Eocene and early Miocene. They were known only in North America until the early Pliocene, 4–5 Ma, when some families crossed the new land bridge to South America, developing there into the modern guanacos, llamas, vicuñas, and alpacas. Then in the early Pleistocene, North American camelids crossed the newly dry Bering Strait into Asia, where they developed into the modern camels. Camelids disappeared from North America soon afterward.

Camelops a late genus of camels, one of a dozen North American camelids that appeared in the Pliocene and became extinct at the end of the Pleistocene.

Camerata a large subclass of stalked crinoids. Its two main orders appeared in the Middle Ordovician; the Diplobathrida disappeared in the Carboniferous, while the Monobathrida continued up to the end-Permian extinction. Cameratans generally had a long, flexible stem, rigidly sutured calyx, and more than ten free arms. See also **Cladida** and **Bobcaygeon**. Middle Ordovician to late Permian.

Cameroceras see **Endoceratidae.**

Campanile an extant genus of very large marine gastropods in the order Sorbeoconcha and family Campanilidae. It has a thick, high-spired, turreted shell with knobs and fine growth lines on the surface. The largest species was *C. giganteum* of the Eocene, which grew to almost 2 feet long. The first campanilids appeared as early as the Late Jurassic, and the family diversified in the Cretaceous and Paleocene. It flourished worldwide from the Eocene to the Miocene, declining then to only one extant species, *C. symbolicum* of Australia. Global distribution, Cretaceous to Recent.

Camptosaurus a genus of midsized ornithopod dinosaurs, formerly called *Camptonotus*. About 26 feet long, it was herbivorous, with a very small head and small, flat teeth, and is estimated to have weighed up to 1 ton. Clawless and basically bipedal, it had four toes on each limb and was a good runner. North America and Europe, Early Jurassic.

Campylognathoides "bent jaw," a basal genus of medium-sized pterosaurs. Its arms are short, but the fourth digit (carrying the trailing edge of the wing) is exceptionally long. The largest species, *C. zitteli*, had a wingspan of 6 feet. *Campylognathoides* had a stout beak and may have hunted on the ground as well as in the air, but like other pterosaurs, it was primarily piscivorous. It is named for the slight upward bend at the tip of its lower jaw. The genus is best known from the Holzmaden Shale. Germany and possibly India, Early Jurassic, 183–180 Ma.

Canadaspis a genus of crustaceans or arthropods in the malacostracan subclass Phyllocarida. It was 1–2 inches long, with a flattened and rounded body protected by an almost circular bivalved carapace. Common in the Burgess Shale and known also in Utah and Nevada, and possibly in China (the uncertain *C. laevigata*). North America and China (?), early to middle Cambrian.

Caninae a subfamily of carnivorous mammals in the order Carnivora and family Canidae. It includes the dogs, wolves, foxes, coyotes, dingoes, and jackals, as well as their most recent ancestors, such as *Leptocyon*. Global distribution, Oligocene to Recent.

Canine conical mammal teeth between the incisors and premolars, adapted for grasping and piercing prey. They are generally in two pairs, upper and lower, and are vestigial in many herbivores.

Caninia a genus of solitary rugose corals in the order Stauriida and family Cyathopsidae. It was cono-cylindrical and lived mainly in shallow lagoons, where it was often affected by storms. Global distribution, Early Devonian to late Permian.

Canobius a genus of small palaeoniscid actinopterygian fish. Three inches long, it is notable for its vertical jaw suspension, as opposed to the diagonal arrangement of other palaeoniscids. Its larger gape allowed it to swallow great volumes of plankton, catching them on its very small teeth, which grew even on its gills. Scotland, Early Carboniferous.

Cantius a genus of early strepsirrhine adapiform primates in the family Notharctinae. Lemur-like, it is known from numerous teeth and jaw fossils. North America and Europe, early Eocene.

Capinatator "seizing swimmer," a genus of large arrow worms in the phylum Chaetognatha. *C. praetermissus* is known from specimens found at the Burgess Shale site and described in 2017. It was 4 inches long and had two dozen mobile grasping spines on each side of its mouth, used to capture prey. Canada, middle Cambrian, 508 Ma.

Capitosauroidea a superfamily of primitive temnospondyl amphibians in the clade Capitosauria; synonym Mastodonsauroidea. Global distribution, Early Triassic to Middle Jurassic.

Captorhinida a paraphyletic order of stem reptiles of the late Paleozoic, formerly called cotylosaurs; see **Pareiasauridae** and **Procolophonidae**.

Captorhinus a genus of small, lizard-like reptiles in the family Captorhinidae. Highly specialized, it was distinguished by a hooked snout with procumbent front teeth; its skull was 5 inches long, and its limbs were slender. Global distribution, early Permian.

Carapace the hard, protective dorsal body covering of many arthropods and some reptiles, such as turtles; it is composed of chitin or bony substances.

Carbonicola a genus of vagrant freshwater clams in the family Anthracosiidae; formerly called *Anthracosia*. Up to 1.5 inches long, it was roughly oval with unequal valves. Several short-lived species are index fossils in the British Coal Measures; Europe, Carboniferous.

Carboniferous the fifth period of the Paleozoic Era, from 359 to 299 Ma. For North American strata, the Carboniferous is divided into two sub-periods: the Mississippian, from 359 to 323 Ma, and the Pennsylvanian, from 323 to 299 Ma; both the Mississippian and the Pennsylvanian are divided into Early, Middle, and Late epochs. The period saw the culmination of a long period of increasing levels of oxygen in the atmosphere, reaching as high as 35%. The Carboniferous globally is noted for coal-bearing beds resulting from large forests. It was also marked by several periods of widespread glaciation, especially in the last half of the period and extending into the Permian. The seed ferns continued to be an important part of the

flora, the first gymnosperms appeared and spread rapidly, and the conifers and ancestors of the cycads appeared near the end of the period. An important development for vertebrates was the evolution of the amniotes. Late in the Carboniferous, these later tetrapods diversified rapidly, one branch producing the first reptiles. Terrestrial arthropods and flora also increased greatly in diversity.

Carcharodon an extant genus of large white sharks in the family Lamnidae; synonym *Carcharocles*. The largest shark known to have lived was *C. megalodon*, which may have grown to a length of more than 60 feet and became extinct only around 50,000 years ago. Cosmopolitan, Miocene to Recent.

Carcharodontosauridae a family of very large theropod dinosaurs, including *Acrocanthosaurus*, *Carcharodontosaurus, Giganotosaurus*, *Mapusaurus, Tyrannotitan*, and others. South and North America, Africa, Asia, and Europe; Early to Late Cretaceous.

Carcharodontosaurus saharicus a species of theropod dinosaurs in the family Carcharodontosauridae. Named for the resemblance of its serrated teeth to those of the shark *Carcharodon*, it reached a length of almost 40 feet and was a top predator. It was as large as *Tyrannosaurus rex* but slightly smaller than *Spinosaurus*. Tunisia and Egypt, Late Cretaceous, 90 Ma.

Cardiocephalus a genus of microsaurian lepospondyl amphibians in the family Gymnarthridae. It was lizard-like, with four short legs and a long tail, and is named for its heart-shaped head. United States, early to middle Permian.

Cardioceras a genus of nektic ammonoids in the order Ammonitida, superfamily Stephanoceratoidea, and family Cardioceratidae. Up to 10 inches in diameter, it is notable for its strong ribs, evolute shell, and prominent crest on the margin. The first appearance of *C. redcliffense* defines the beginning of the Oxfordian Age of the Late Jurassic at 163.5 Ma. Europe and Canada, Jurassic, 163.5–158 Ma.

Caridea an infraorder of shrimps, decapods in the class Malacostraca and suborder Pleocyemata. Their fossil record is sparse, and the earliest are *incertae sedis*. Global distribution, Early Devonian to Recent.

Carnassial teeth the last premolars of the upper jaw and the first true molars of the lower jaw of most carnivores. They are sectorial, adapted for cutting rather than tearing, and are larger and longer than adjacent teeth.

Carneyella a genus of edrioasteroid echinoderms in the order Isophorida and family Hemicystitidae. Disc-shaped and almost an inch across, it had five slender and sharply curving ambulacra. It attached itself to the substrate, frequently to brachiopods. United States, Early Ordovician, 448 Ma.

Carnivora a diverse order of placental mammals in the clade Laurasiatheria. The primary suborders are the Caniformia, Feliformia, and Pinnipedia. The earliest were the Miacidae, which appeared in North America in the late Paleocene, and their descendants radiated rapidly throughout the world. Classified on the basis of dentition, some members of the order are omnivorous, while others are herbivorous. Paleocene to Recent.

Carnosaur a general term for a polyphyletic group of many large predatory dinosaurs, especially the allosaurs. Some now refer to Carnosauria as an infraorder including only the allosaurs and their closes kin. A large head, a short neck, generally short forelimbs, and neural spines are characteristic structures of the group. Global distribution, Jurassic to Cretaceous.

Carnotaurus a genus of large carnivorous dinosaurs in the family Abelisauridae, characterized by a large head, two short but stout horns above the eyes, a short and deep snout, relatively small teeth, and very small vestigial forelimbs. *Carnotaurus sastrei* is the type species, known from a well-preserved skeleton found by Paul Sereno in Patagonia. Argentina, Late Cretaceous, 72–70 Ma.

Carnufex carolinensis an ancestral crocodile, among the earliest crocodylomorphs, known from a North Carolina specimen described in 2015, with a skull, spine, and forelimbs. It was about 9 feet long; judging from size and weight distribution, it may have stood on its hind legs. Its diet consisted of early mammals and small armored reptiles. United States, Late Triassic, 231 Ma.

Carpoidea see **Homalozoa**.

Cassiduloida an extant order of atelostomate sea urchins, echinoids in the superorder Neognathostomata, closely related to the sand dollars, the Clypeasteroida. As adults they have no lantern and generally have a suboval, flattened shape. Widespread in the Mesozoic but declining since then, Early Jurassic to Recent.

Cast see **mold.**

Castor canadensis the North American beaver, a genus of rodents in the family Castoridae. About 3 feet long and almost extinct after centuries of trapping for its pelt, it has recovered. It has many subspecies but is not related to *Aplodontia*, the "mountain beaver." North America, Miocene to Recent.

Castorocauda lutrasimilis a fish-eating species of Jurassic semiaquatic mammaliaforms in the order Docodonta. It was similar to beavers and otters but not related to them. Recorded as the earliest semiaquatic mammal, dated between 170 and 165 Ma, it is the largest-known mammaliaforme of the Jurassic at 1–2 pounds and almost 2 feet long. It had webbed feet; a flat, beaver-like scaly tail; otter-like vertebrae; and teeth like those of a seal. Yanliao biota, China, Northern China, Middle Jurassic.

Castoroides the largest beaver, a genus of very large rodents in the subfamily Castoroidinae. Almost 10 feet long and about 200 pounds, it had teeth that were not well-adapted for cutting wood, and there is no evidence that it constructed dams, as modern beavers do. United States and Canada, early to late Pleistocene.

Catarrhini an infraorder of anthropoid primates that includes men, apes, and Old-World monkeys (see also **Platyrrhini**). The Catarrhini have nostrils that face downwards, and most have tails, but they are nonprehensile. They diverged from the Platyrrhini in the late Eocene or early Oligocene but remained primarily alike because of parallel evolution. The Catarrhini are subdivided into Cercopithecidae (Old-World monkeys), Hominidae (humans, gorillas, chimpanzees, orangutans, and australopithecines), and Hylobatidae (gibbons). Eocene to Recent.

Catastrophism see **uniformitarianism**.

Catenipora a large genus of tabulate corals in the family Halysitidae; Baltic, Late Ordovician to early Silurian.

Cathaymyrus a genus of early Cambrian cephalochordates. Similar to *Pikaia*, it is long and slender (1–2 inches) and seems to have a notochord in the depression along the center of its back. Chengjiang biota, China, ca. 518 Ma.

Catopithecus browni possibly the earliest-known anthropoid primate, a species of catarrhine primates in the family Oligopithecidae. *Catopithecus* was squirrel-sized and is known from several tooth and skull fragments found at Fayum. It is characterized by shovel-shaped upper front teeth, a flattened face, forward-looking eye sockets, and a fused forehead bone; the latter is a key difference between lemurs and the higher anthropoid primates. All known specimens are dated at about 36 Ma. Egypt, late Eocene.

Caudipteryx "tail feather," a species of theropod dinosaurs, considered a basal oviraptorosaur. Known from two specimens, one complete, it had considerable plumage, including a large tail fan. However, although it was birdlike and the size of a peacock, its body was covered with only short feathers, and it probably lacked the aerodynamic qualities required for flight. Dated at 125 Ma, it is one of several feathered dinosaurs in the Jehol Biota. China, Early Cretaceous, 130–122 Ma.

Cavellinidae a family of podocopan ostracods in the order Platycopida and superfamily Cytherelloidea; global distribution, Silurian to Triassic.

Caytoniales an order of Mesozoic seed ferns in the division Pteridospermatophyta, important especially because of their possible transitional relationship to the angiosperms. Their four-part palmate leaves (form genus *Sagenopteris*) are similar to some later flowering plants, and they bear a carpel-like case containing seeds (form genus *Caytonia*). A direct relationship is still unclear, however, and they may be gymnosperms. Global distribution, Early Triassic to Early Cretaceous.

Cebochoerus a genus of basal artiodactyl mammals in the extinct superfamily Dichobunoidea and family Cebochoeridae. Piglike but unspecialized, the cebochoerids may have an ancestry in the little-known Helohyidae. Europe, middle Eocene to early Oligocene

Cedar Mountain Formation a rock formation in east central Utah, especially important for its dinosaurs. Overlying the Morrison Formation, it was laid down at the end of the Lower Cretaceous.

Cedrobaena putorius a species of early cryptodire turtles in the family Baenidae; originally named *Plesiobaena putorius.* United States, Late Cretaceous to early Paleocene.

Cell division see **mitosis**.

Cenophyticum term sometimes used for a paleobotanic division of time roughly corresponding to the Cenozoic Era and characterized by the plant life of the Cenozoic. The abundant angiosperm floras of the Late Cretaceous are also generally considered cenophytic.

Cenozoic Era the third division of Phanerozoic geologic time, following the Paleozoic and Mesozoic and extending to the present. See also **Geologic Time Scale.**

Centronellidina a suborder of articulate brachiopods in the order Terebratulida. They have a primitive loop structure and an incurving ventral beak. North and South America, Early Devonian to late Permian.

Centrosaurinae a subfamily of horned ornithischian dinosaurs in the family Ceratopsidae. Medium-sized, averaging less than 20 feet long, these herbivores ranged across western North America from Alaska to Arizona, with at least one species, *Sinoceratops*, found in China in 2010. Several embryos have been found in nest sites. See also **Chasmosaurinae**. North America and China, 84–66 Ma.

Centrosaurus a genus of ceratopsian dinosaurs in the subfamily Centrosaurinae. The type species *C. apertus* was found in southeastern Alberta, where great numbers of the genus have since been found. A medium-sized ceratopsian, it had a large nasal horn and several small horns on its frill, two of them pointing forward. The frill has large fenestrae. *Centrosaurus* is not related to *Kentrosaurus*, a stegosaur of the Late Jurassic. Canada, Late Cretaceous, 77–76 Ma.

Cephalaspis "headshield," a genus of freshwater ostracoderm fish in the class Osteostraci. These primitive armored fish were about 1 foot long and had a flattened headshield and large pectoral fins. With a mouth located under its head, *Cephalaspis* probably fed on detritus on the bottom of streams. North America and Europe, Early Devonian.

Cephalic referring to the head.

Cephalochordata the least numerous subphylum of the chordates, characterized by a stiff notochord throughout life, as well as a dorsal nerve cord and gill slits. They were generally fish-like marine animals with a notochord the length of the body, which ranges from 2 to 6 inches long. Because they had no hard parts, the fossil record is sparse. However, it extends from *Pikaia gracilens* of the Burgess Shale to the modern lancelets, including dozens of modern genera in the Branchiostomiformes (also called Amphioxiformes). See also **Tunicata**. Middle Cambrian to Recent.

Cephalodiscidae the largest family of small, wormlike animals in the class **Pterobranchia**, *q.v.*; Late Ordovician to Recent.

Cephalogale "helmet head," a genus of carnivorous mammals in the family Ursidae and subfamily Hemicyoninae. Among the earliest ancestors of bears, it was doglike and the size of a raccoon, and later species became omnivorous. *Cephalogale* appeared in Eurasia in the middle Oligocene and in North America in the early Miocene; it was replaced in the Miocene by more advanced ursids.

Cephalon the front section of an arthropod. In trilobites the cephalon consists of specialized parts, such as the eyes and glabella, and also the free cheeks in most genera.

Cephalopoda an extant class of marine mollusks that includes ammonoids, nautiloids, and coleoids. They are probably descended from a monoplacophoran such as ***Knightoconus**, q.v.* Global distribution, late Cambrian to Recent.

Cephalothorax the anterior part of the body of spiders and some other chelicerate arthropods; synonym prosoma. Typically covered by a non-segmented carapace, it contains the mouth parts, eyes, and other sensory organs, fused with the limb-bearing central part of the body.

Ceramoporidae a family of bryozoans in the extinct order Cystoporata. The early Ceramoporinae were simple encrusting organisms, while the later Crepiporinae had branching colonies. North and South America, Europe, and Asia; Ordovician to Late Devonian.

Ceratiocarididae a family of phyllocarid crustaceans in the order Archaeostraca. A new species, *Ceratiocaris winneshiekensis*, was reported in 2016 as the earliest-known representative of the family. North America, Middle Ordovician to Silurian.

Ceratitida an order of ammonoids that includes most of the Triassic ammonoids (about 400 genera, excluding those of the subfamily Phylloceratina, which are ammonitid). They are generally recognized by the ceratitic suture pattern of smooth

saddles and serrate lobes, with sometimes strongly indented loops. Although more complex than the earlier goniatitic pattern, it is less complex than the ammonitid pattern characteristic of most Jurassic and Cretaceous ammonoids. Global distribution, Permian to Triassic.

Ceratogaulus a genus of fossorial horned rodents in the family Mylagaulidae, the only known horned rodent; synonym *Epigaulus*. Related to *Aplodontia*, the modern "mountain beaver," it was about a foot long and generally marmot-like. It is notable for a pair of sturdy, sharp horns on the snout, between the nostrils and the eyes. The function of the horns is disputed; they may have aided in digging but were probably used mainly for defense. *Ceratogaulus* is an example of convergent evolution with the unrelated *Peltephilus* of South America, the only other known fossorial horned mammal. Western North America, late Miocene to early Pleistocene.

Ceratomorpha a suborder of perissodactyl mammals that includes the Tapiroidea and Rhinocerotoidea, distinguished by a strong transverse crest on the molars. Global distribution, late Paleocene to Recent.

Ceratopsia "horned face," a large suborder of herbivorous ornithischian dinosaurs that originated in the Late Jurassic and thrived in the Cretaceous across the Northern Hemisphere. The first-named specimens were given the names *Ceratops* and *Proceratops*, but these are now considered nomina dubia since the specimens have all been assigned to later genera or discarded as too fragmentary. Only 3 to 7 feet long, the early ceratopsians (such as the basal *Yinlong* of the late Jurassic and the Psittacosauridae of the Early Cretaceous) were hornless and bipedal. The later genera became quadrupedal as they grew larger, developing a great variety of horns and frills on the head and neck. The family Ceratopsidae of North America was the most advanced, including the subfamilies Centrosaurinae and Chasmosaurinae. Europe, and Asia; Late Jurassic to Late Cretaceous, 160–66 Ma.

Ceratosauria a large clade of theropod saurischian dinosaurs that arose around 225 Ma. Carnivorous, generally bipedal, and at first quite small, by the Middle Jurassic they had evolved into larger species up to 9 feet long and by the Late Jurassic others as long as 19 feet. The early ceratosaurs gave rise to other groups, principally the Abelisauridae. Late Triassic to Late Cretaceous.

Cercidiphyllum an extant genus of riparian trees that was common in the early Cenozoic in the northern areas of Asia, Europe, and North America. A relative of the modern *Katsura* tree, it is now found only as two species in Eastern Asia.

Cercopithecoidea the Old-World monkeys, including macaques, mandrills, and baboons. They are grouped with humans and great apes in the infraorder Catarrhini; early Miocene to Recent.

Cerebavis cenomanica a disputed species of early birds known from a single braincase, putatively a basal ornithurine; Russia, Early Cretaceous, 93 Ma.

Ceriantharia a small subclass of anthozoan cnidarians, consisting of only one order of the same name. Called tube-dwelling anemones, they are classified as a sister group of the corals. Ceriantharians are almost absent from the fossil record because they have no hard parts, but an early Cambrian microfossil named *Eolympia pediculata* was described in 2010 and classified as a ceriantharian.

Ceratoid hornlike or horn-shaped.

Cerioid of corals, having a tightly packed structure of polygonal corallites sharing common walls.

Cerithium a speciose, extant genus of marine gastropod mollusks in the clade Sorbeoconcha and family Cerithiidae, highly varied and widespread since the Cretaceous. Small to medium-sized, cerithiids are high-spired and generally conical, with whorls often nodular and highly ornamented. Global distribution, Triassic to Recent.

Cervalces alaskensis the stag-moose, a large ancestor of the modern moose; Alaska, late Pleistocene.

Cervidae a family of cloven-hoofed ruminant ungulate mammals in the order Artiodactyla, distinguished from the Bovidae by their solid, deciduous, generally branching antlers. A probable early ancestor is *Diacodexis* (middle Eocene), and one of the earliest cervids is *Leptomeryx* (Eocene to Miocene). Global distribution, Oligocene to Recent.

Cetacea an extant order of marine artiodactyl mammals that includes the modern whales, porpoises, and dolphins. Long thought to be descended from the large group of protoungulate land mammals called mesonychids, the earliest ancestral whales are now generally considered more closely related to the hippopotamuses. The direct ancestors of *Pakicetus* and other early whales are still unclear, however. For the evolution of marine mammals, see ***Aegyptocetus, Ambulocetus, Basilosaurus, Cetancodonta, Indocetus, Indohyus, Pakicetus, Protocetus,*** and ***Rodhocetus***. Global distribution, early Eocene to Recent.

Cetancodonta a proposed term for a clade including cetaceans and hippopotamuses; synonym Whippomorpha. Global distribution, Eocene to Recent.

Cetartiodactyla the clade including cetaceans and other artiodactyls.

Chaetae chitinous bristle-like setae found on some insects, especially characteristic of polychaete annelid worms.

Chaetetes a genus of demosponges in the family Chaetitidae, widespread from the Ordovician to the Jurassic.

Chaetetids small tubular organisms formerly classified as anthozoans, specifically tabulate corals, or even as algae; now considered a polyphyletic group of demosponges. They generally formed globular colonies composed of fused tubular skeletons, in mounds sometimes as large as 10 feet. Appearing in the Ordovician and widespread through the Permian, they had been thought to be extinct at the end of the Jurassic, but some extant species (such as *Acanthochaetetes wellsi*) have been discovered off the northeastern coast of Australia.

Chaetognatha a phylum of arrow worms known from the Cambrian to the present. Their record is poor because of a paucity of whole-body fossils, but they are a significant zooplanktonic component in modern oceans. See also ***Capinatator*** and ***Eognathacantha***. Cambrian to Recent.

Chalicotherioidea a superfamily of clawed perissodactyl mammals in the suborder Ancylopoda, comprising two families, the widespread Chalicotheriidae and the Eomoropidae, which are known mainly from Asia. Some genera were about the size of a horse, probably browsers, but their habits are not completely known. Most had forelimbs that were longer than the hindlimbs. Their claws, often long, made movement awkward, but some may have been able to raise the claws enough to walk on their pads. They are related to brontotheres, horses, rhinoceroses, and tapirs. Holarctic distribution, early Eocene to Pleistocene.

Chamitataxus a genus of caniform carnivores in the family Mustelidae and subfamily Taxideinae. Known only from a skull found in New Mexico, *Chamitataxus* existed alongside *Taxidea*, the modern North American badger, in the late Miocene.

Champsosaurus a genus of diapsid reptiles in the order Choristodera and family Champsosauridae, widespread in the Late Cretaceous and Paleocene. Superficially similar to the modern gharial, *Champsosaurus* was almost completely aquatic. Its jaws were adapted to catching fish, with powerful muscles attached to its broad skull. It was generally about 5 feet long, although the largest species, *C. gigas*, grew to 12 feet. Champsosaurs are significant especially for specimens found near Ellesmere Island, high in the Canadian Arctic. North America and Europe, Late Cretaceous to Eocene.

Chañares Formation an important Late Triassic site in Northwestern Argentina. It is notable for tetrapods and archosaurians, including possible ancestors of the earliest dinosaurs. The Santa Maria Formation of Southern Brazil also has outcrops of the same strata. Early Carnian, 235–233 Ma.

Chancelloriidae an enigmatic group of sponge-shaped Cambrian organisms, possibly related to *Halkieria*. Sessile and probably filter feeders, sometimes found attached to other organisms; they had a bag-shaped body covered with spiny sclerites and are 1–8 inches long and narrow at the bottom. See also **Guanshan biota**. Global distribution, early to late Cambrian.

Chaohusaurus geishanensis a species of ichthyopterygians in the order Grippidia and family Grippiidae, generally considered a basal ichthyosaur. Known from several almost complete specimens, one of which is notable for containing the remains of three embryos, one in the birth position. China, Early Triassic, 248 Ma.

Chaoyangsaurus youngi an unusual species of marginocephalian ceratopsian dinosaurs in the family Chaoyangsauridae. Along with *Yinlong*, it is among the earliest ceratopsians. Known from the lower jaw, the front part of the skull, and a partial spine, it probably had no horns or frill and is estimated at 2–3 feet long and 25–30 pounds. China, Late Jurassic, 150 Ma.

Character a distinctive heritable trait or property that defines a taxon, differentiating it from other taxa. A character may be morphological, behavioral, molecular, or physiological.

Charassognathus a monospecific genus of small cynodont therapsids. The earliest-known cynodont, *C. gracilis* is known only from a skull and one leg but is estimated to have been 1–2 feet long. South Africa, late Permian, 260 Ma.

Charnia an enigmatic genus of Ediacaran fossils. It was benthic, probably in a deepwater environment and was superficially similar to sea pens. The central stalk rose from a bulbous holdfast set in sediment. The long, narrow fronds display a series of fine ridges along the entire length, up to 6 feet. It is found in association with *Aspidella* and may have been attached to it. *Charnia* is named for Charnwood Forest in England, where it was first found. Europe and North America, 579–555 Ma.

Charniodiscus a feather-shaped Ediacaran fossil, the tallest 1–2 feet high. Like its relative *Charnia*, it was benthic and sessile, with a central branch rising from a bulbous or disc-shaped holdfast. It was a filter feeder with about 20 secondary branches on each side of the central shaft, with polyps on each branch. *Charniodiscus* is morphologically similar to the pennatulaceans of the Cambrian, but its affinities are uncertain. Global distribution, 565–555 Ma.

Charophyceae a class of freshwater green algae in the division Charophyta; Silurian to Recent.

Charophyta a division of calcareous freshwater green algae, closely related to plants. The gyrogonites of some charophytes are stratigraphically important. Early Silurian to Recent.

Chasmatosaurus see ***Proterosuchus***.

Chasmosaurus a genus of medium-sized ceratopsid dinosaurs in the subfamily Chasmosaurinae. Up to 17 feet long and herbivorous, *Chasmosaurus* is notable for very large fenestrae in a large neck frill and by a short nasal horn. North America and Asia, Late Cretaceous, 78–75 Ma.

Chaunograptus a possible genus of graptolites, the earliest known, common in the Burgess Shale, 508 Ma. *Chaunograptus sphaericola* has been identified in a Devonian deposit in Estonia. North America and Europe, middle Cambrian to Devonian.

Cheiracanthus a genus of freshwater acanthodian fish in the family Acanthoessidae. Deep-bodied and about a foot long with a highly heterocercal tail, it is notable for having only one dorsal fin. Whole-body specimens are known from Europe, and its distinctive scales have been found worldwide. Global distribution, Middle Devonian.

Cheirolepis a basal genus of freshwater actinopterygian fish, the only genus in the family Cheirolepidae. Almost 2 feet long, it is characterized by a heterocercal tail fin, a moveable jaw that gave it a wide gape, and ganoid scales locked together in a peg-and-socket design. See also ***Moythomasia*** and ***Meemannia***. North America and Europe, Middle to Late Devonian.

Cheirurus a genus of phacopid trilobites, the type genus of the family Cheiruridae. From 2 to 3 inches long, the cheirurids are notable for long, swept-back and curving spines extending from the cephalon and the pygidium. Global distribution, late Cambrian to Middle Devonian.

Chelicerata a class of arthropods that includes the arachnids, scorpions, eurypterids, horseshoe crabs (Xiphosurida), and possibly the sea spiders (Pycnogonida), all of which have living representatives. The earliest known seems to be ***Habelia***, *q.v.*, known from the Burgess Shale and newly described in 2017 as a chelicerate. Until then the earliest unchallenged ones were eurypterids from the Middle Ordovician. Chelicerates are named "claw horn" because of their principal synapomorphy, jointed appendages (chelicerae) which are usually pincers. Global distribution, Cambrian to Recent.

Chelonian see **Testudines**.

Chelydridae a small family of cryptodiran turtles. It was once known throughout the Northern Hemisphere, but its range has shrunk so that only two genera of snapping turtles of North and South America are still extant. North America, Europe, and Asia; Late Cretaceous to Recent.

Chengjiang biota an important assemblage of early Cambrian fossils found in several Konservat-Lagerstatten in the Maotianshan Shales. Although the dating of these formations is difficult and uncertain, the approximate date is between 518 and 515 Ma, at least 7 million years earlier than the Burgess Shale. The strata are mostly finely bedded mudstones and preserve a great variety of soft-tissue fossils. In contrast to the organisms of the Burgess Shale, those in the Chengjiang sites are generally autochthonous, preserved in their living position. One of the largest groups is the arthropods, many of them bivalved crustaceans (see ***Kunmingella***). Some, such as *Stromatoveris* have been connected with Ediacaran organisms. Several, such as *Waptia*, *Liangshanella*, and *Anomalocaris*, are congeneric with the Burgess biota, and species of other organisms, such as the lobopods *Hallucigenia* and *Aysheaia*, are also closely related. See also ***Misszhouia*** and **Qingjiang biota**. Southern China, early Cambrian, 518–515 Ma.

Chengjiangocaris kunmingensis a species of crustacean-like animals in the family Chengjiangocarididae. One of several shrimplike species known only from the Chengjiang biota, it is notable especially for details indicating a central nervous system. See also ***Fuxianhuia***. China, early Cambrian, 516–513 Ma.

Chesaconcavus a genus of barnacles in the extant family Balanidae and subfamily Concavinae; North America and Europe, Miocene to Pliocene.

Chevrotain see **Tragulidae**.

Chicxulub asteroid see **Cretaceous extinction** and **Bowman**.

Chileata one of the four extinct classes of articulate brachiopods in the subphylum Rhynchonelliformea. Notable for a large perforation in the ventral valve, chileatans have both strophic or astrophic hinges. The class is generally considered to contain two orders, Chileida and Dictyonellida. Global distribution, Cambrian to Permian.

Chilgatherium a genus of proboscideans in the family Deinotheriidae. Known only from some molar teeth, it is estimated to have resembled a large tapir, perhaps 5–6 feet high at the shoulder, and is considered the ancestor of the larger *Prodeinotherium* and *Deinotherium*. Ethiopia, late Oligocene, 28–27 Ma.

Chilobolbinidae a family of dimorphic ostracods in the suborder Beyrichicopina and superfamily Hollinoidea, typically with a frill and a straight hinge; Ordovician to Silurian.

Chilopoda an extant class of myriapods that includes the centipedes. Carnivorous and venomous, with robust jabbing chelicerae; they have only one pair of legs on each body segment. Global distribution, Silurian to Recent.

Chimerarachne yingi a species of very small arachnids that possesses similarities to both spiders and their early arachnid ancestors. It is known from only half a dozen specimens found in Burmese amber and dated just before 100 Ma, long after the early spiders of the order Uraraneida. Like eurypterids, its body is segmented and it has a tail spine longer than the body; its entire length is less than half an inch. Its appearance is spiderlike, and it seems to have silk-producing spinnerets and male sex organs like those of spiders. Burma, Early Cretaceous.

Chindesaurus a genus of theropod dinosaurs in the family Herrerasauridae. One of the first true dinosaurs, it was up to 7 feet long, bipedal, and carnivorous. *Chindesaurus* is known primarily from several partial skeletons found in the Chinle Group of the southwestern United States. North America, Late Triassic, 221–216 Ma.

Chiniquodon a genus of advanced cynodonts in the family Chiniquodontidae. About 2 feet long, it had a robust skull with prominent canine and shearing teeth. Brazil, Argentina, and Madagascar; Middle to Late Triassic.

Chiniquodontidae a family of advanced carnivorous cynodonts, closely related to the immediate ancestors of mammals. They ranged from 1 to 2 feet long and have a robust skull. See also ***Aleodon*** and ***Probelesodon***. South America, Europe, and Africa; Middle to Late Triassic.

Chinle Group biota a *Late* Triassic terrestrial assemblage of fossils from scattered outcrops of Chinle Group rocks of Arizona, New Mexico, Colorado, and Utah. The most familiar examples are the dinosaur *Coelophysis*, the therapsid *Placerias* (best known from the Placerias Quarry in Arizona), the rauisuchian reptile *Postosuchus*, and the petrified wood of trees in the Araucariaceae. The biota also includes many other reptiles, amphibians, invertebrates, fish, and desert plants. Southwestern United States, Late Triassic, 222–212 Ma.

Chiosella timorensis a species of conodonts whose first appearance is generally taken to mark the beginning of the Middle Triassic at 247.2 Ma; Romania and China.

Chippewaella patellitheca a species of primitive snaillike mollusks, possibly the earliest-known gastropod. Known only from specimens found in Wisconsin, it has a round, cap-shaped shell about an inch in diameter. See also ***Strepsodiscus.*** United States, late Cambrian, 500 Ma.

Chirodus a genus of actinopterygian fish in the extinct suborder Platysomoidei and family Chirodontidae. It was deep-bodied with very short dorsal and pectoral fins and a crushing dentition. Europe and North America, Carboniferous to Triassic.

Chirognathidae a family of conodonts in the suborder Prioniodinina. Possessing multiple denticles on the teeth, they are among the earliest of the suborder. Global distribution, Ordovician.

Chiroptera "hand wing," the bats. The order is divided into two suborders, Megachiroptera (large frugivorous bats that do not use echolocation) and Microchiroptera (small echo-locating bats, generally insectivorous). The classification of bats is disputed, but they are generally considered closer to primates than to rodents. See also ***Icaronycteris*** and ***Onychonycteris***. Global distribution, early Eocene to Recent.

Chitin a fibrous polysaccharide material that composes the exoskeleton of arthropods, spiders, insects, and crustaceans; it is present also in parts of many other organisms, *e.g.*, fish scales and insect wing scales.

Chitinozoans an enigmatic group of middle Paleozoic microfossils. Distinctively flask-shaped, they may be eggs or a juvenile stage of unknown marine animals, possibly orthocone cephalopods. Occurring worldwide and especially abundant in Ordovician and Silurian strata, they are important index fossils because of their wide distribution and rapid evolution. Early Ordovician to early Mississippian.

Chitons see **Polyplacophora**.

Choeropotamus a genus of piglike entelodont artiodactyl mammals, the only genus in the family Choeropotamidae. It is related to the Cebochoeridae and possibly descended from the little-known Helohyidae. Europe, late Eocene.

Choia a genus of demosponges in the order Monaxonida. About an inch wide, its conical body was surrounded by a thicket of spicules, with some species resembling stars. It was originally thought to have rested on the seafloor but is now believed to have floated, attached to the substrate by three long spines. See also ***Coronacollina***. Canada, United States, China, and Africa; Cambrian to Ordovician.

Chondrostei a paraphyletic extant subclass of primarily cartilaginous fishes in the class Actinopterygii. The chondrosteans flourished in the late Paleozoic and the Triassic, declining in the Cenozoic. Some Mesozoic families have essentially ossified skeletons and other similarities to the teleosts, so that the modern chondrosteans' cartilaginous condition is probably derived. Cosmopolitan, Silurian to Recent.

Chonetes a long-lived genus of articulate brachiopods in the order Productida and family Chonetidae. About an inch long and relatively flattened, but with a slightly convex pedicle valve, *Chonetes* is marked by a row of short, angled spines along its margin that it used to anchor itself. Global distribution, Late Ordovician to Middle Jurassic.

Chordata the phylum of deuterostome organisms that includes the subphyla Vertebrata, Cephalochordata, and Tunicata. Chordates are characterized by a notochord, a cartilaginous rod down the length of the body; a hollow dorsal nerve cord; pharyngeal apertures (gill slits or pouches); and a tail at some life stage. Early Cambrian to Recent.

Choristodera an order of semiaquatic diapsid reptiles, possibly in the Archosauromorpha. Similar to modern gharials, the choristoderans are represented principally by the families Champsosauridae and Simoedosauridae, which appeared in the Cretaceous and survived the end-Cretaceous extinction into the middle Eocene. North America, Europe, and Asia; Middle Jurassic to Miocene.

Chromogisaurus a monospecific genus of sauropodomorph dinosaurs in the family Guaibasauridae. About 7 feet long and dated at 231 Ma, it is one of the earliest dinosaurs. *Chromogisaurus novasi* is known from one specimen, a partial disarticulated skull and skeleton found in a middle Carnian layer of the Ischigualasto Formation. Argentina, Late Triassic.

Chronocline a time series of fossil specimens showing transitional morphological changes in a taxon in successive strata.

Chronoperates paradoxus "puzzling time wanderer," a problematic Paleocene fossil jaw from Alberta. Now considered vaguely a symmetrodont therapsid, it was originally thought to be an extremely late-surviving cynodont, the therapsid ancestors of mammals which became extinct 100 million years earlier, midway through the Cretaceous. Canada, late Paleocene.

Chrysochloridae a family of insectivorous burrowing mammals in the order Afrosoricida. Called golden moles, they are so like the marsupial moles of Australia that some researchers have claimed they are closely related. Southern Africa, early Miocene to Recent.

Chuaria circularis a species of Ediacaran acritarchs. With a diameter of about a sixteenth of an inch, it is a large acritarch found prominently in the upper strata of the Grand Canyon Supergroup. North America, Eurasia, and Africa; Ediacaran, 635–542 Ma.

Cidaroida an extant order of primitive sea urchins in the subclass Perischoechinoidea. The only order of the subclass to survive into the Cenozoic Era, it is distinguished by large and widely separated primary spines. Global distribution, early Permian to Recent.

Cifelliodon a monospecific genus of mammaliaforms placed tentatively in the order Haramiyida and family Hahnodontidae. *C. wahkarmoosuch* is known from a single skull found with several dinosaur specimens in the Cedar Mountain Formation

of Utah, in the Yellow Cat Member, which provides its species name. The broad, shallow skull is about an inch long and bears transitional features between early mammaliaforms and true mammals. *Cifelliodon* had a small brain, large olfactory bulbs, and bat-like teeth; it is estimated to have been the size of a small pika. It may be akin to the Gondwanatheria, with possible implications for the date of separation of Gondwana from Pangaea. See also **paleogeography**. United States, Early Cretaceous, 130–125 Ma.

Cimexomys a genus of multituberculate mammals, poorly known but tentatively placed in the suborder Cimolodonta. Western North America, Late Cretaceous to Paleocene.

Cimolesta a proposed order of eutherian mammals, related to several other early groups of mammals such as the creodonts, dinoceratans, and pantodonts; North America, Europe, Asia, and Africa; Cretaceous to Eocene.

Cimolestidae a family of small nonplacental mammals in the order Cimolesta. Generally scansorial insectivores, they were closely related to the taeniodonts. Holarctic distribution, Cretaceous to Eocene, 70–50 Ma.

Cimoliopterus a genus of pterodactyloid pterosaurs with a wingspan of about 16 feet. The two species are *C. cuvieri* (England) and *C. dunni* (Texas), and they are closely related to a slightly older pterosaur from Texas, *Aetodactylus halli*. Early Cretaceous, 94 Ma.

Cinctans an enigmatic group of slow-moving early Paleozoic animals thought to be non-pentameral basal echinoderms, sometimes called Homostelea. Only a few centimeters long, they are composed of interlocking, generally rectangular plates arranged in an oval shape resembling a small tennis racket, with a short extension at the narrow end. Europe and North Africa, middle Cambrian, 509–497 Ma.

Cingulata an order of armored xenarthran mammals that includes the modern armadillos and the extinct pampatheriids and glyptodonts. South and North America, late Paleocene to Recent.

Cirri singular *cirrus; also spelled cirrhi*. Cirri are slender, tentacle-like appendages in many animals, especially in crinoids, octopi, barnacles, and other marine invertebrates. In crinoids, cirri extending from the calyx or stalk are often used for attachment to the substrate.

Cirripedia the barnacles, a subclass of marine crustacean arthropods traceable to the Cambrian but uncommon in the fossil record until the late Cenozoic. The shell is typically constructed of six triangular plates in a conical shape. They are generally sessile and cemented to the substrate by a firm base, living in the highly erosional tidal zone. Since only a few genera live in deepwater, they are sometimes

used as indicators of paleodepths, estimated by the degree of disarticulation of the shells. See also ***Chesaconcavus*** and ***Priscansermarinus***. Global distribution, middle Cambrian to Recent.

Citipati a genus of theropod dinosaurs in the family Oviraptoridae. At about 160 pounds and 8 feet long, it was a carnivore similar to *Troodon* and *Oviraptor*, notable for birdlike reproductive behavior. It laid 7-inch-long eggs and had a rounded crest. Mongolia, Late Cretaceous, 84–75 Ma.

Clade a monophyletic group of two or more species with a common ancestor, as well as all the other descendants of that ancestor.

Cladida a contentious group of crinoids, traditionally considered an order in the discarded subclass Inadunata but now placed in the subclass Camerata, with many former cladid families moved to other orders.

Cladistics a method of reconstructing the phylogeny of organisms on the basis of shared derived characters, indicating a common ancestry.

Cladodont dentition broad-based teeth with a large primary cusp, a broad base, and several secondary cusps. Cladodont teeth are common in Paleozoic sharks such as *Cladodus* but little known after the Triassic.

Cladodus a genus of small sharks in the family Ctenacanthidae. One of the earliest examples of cladodont dentition, which was effective for grasping prey and swallowing it whole. Global distribution, Early Carboniferous to Permian.

Cladogenesis see **anagenesis**.

Cladogram a branching diagram that shows evolutionary relationships among groups of organisms, placing the most closely related taxa on adjacent branches.

Cladoselachidae an early family of sharks. About 6 feet long and almost scaleless, they were cartilaginous and had a cladodont dentition, two dorsal fins, and large and paddle-like pectoral fins; they had no anal fin. North America, Devonian to Permian.

Cladoxylon a genus of early vascular plants in the large group called cladoxylopsids. It grew only about a foot high and may have been leafless, but its central stem marks it as a forerunner of sizeable trees that appeared in the Devonian. Global distribution, Middle Devonian to Early Carboniferous.

Claraia a genus of thin-shelled, scallop-like bivalves in the order Pectinoida. Along with the similar *Eumorphotis*, it is called a “paper pecten” and is one of several disaster taxa of bivalves that survived the Permian extinction and flourished in the anoxic environments of the Early Triassic. *Claraia* became ubiquitous at the

beginning of the Triassic before declining and disappearing at the end of the Anisian age. Global distribution, late Permian to Middle Triassic, 265–242 Ma.

Clarkecaris a genus of crustaceans in the order Anaspidacea and proposed family Clarkecarididae; Brazil, early Permian.

Clarno Nut Beds a botanically rich site near John Day, Oregon. Although the Nut Beds of the Clarno Formation contain few vertebrate fossils, they are one of the most important paleobotanical sites in the world. They contain hundreds of well-preserved botanical fossils from a large forest of the Eocene, dated at 44 Ma. United States, middle Eocene.

Clathropteris meniscioides a species of reticulate ferns, known worldwide from the Late Triassic to Middle Jurassic.

Clavatoraceae a Mesozoic family of charophytic algae. Several species representing gradual evolutionary changes are index fossils from the Late Jurassic to the end of the Cretaceous.

Cleoniceras a genus of large ammonoids in the order Ammonitida and family Hoplitidae. Known in five species, it grew up to 10 inches high and 3–4 inches across the aperture. *Cleoniceras* was moderately involute, with a relatively smooth surface for a hoplitid. Its sutures form a low sine wave, and its surface has a complex ammonitid dendritic pattern. The type species, *C. cleon*, is a popular commercial specimen, especially polished pieces from Madagascar. Global distribution, Early Cretaceous, 113–101 Ma.

Cleveland-Lloyd Dinosaur Quarry an important Late Cretaceous site, especially for dinosaurs. Located on the site of a boggy marsh dated at 147 Ma, the quarry's Morrison Formation strata have produced thousands of disarticulated dinosaur bones. It is especially noted for the large number of *Allosaurus* specimens. There are also dinosaur tracks in the vertical cliffs and specimens from all other vertebrate classes. Of the dinosaurs, many more carnivores than herbivores are represented. Only a few whole skeletons have been found, evidently because of the slow turbidity of the clay sediments in the bog. Central Utah, Late Jurassic.

Climacograptus a genus of scandent graptolites important as index fossils in the Ordovician, distinguished by a single serrated stipe; Middle Ordovician to Lower Devonian.

Climatiiformes an order of small, spiny acanthodian fish, only about 3–4 inches in length. They had several stout spines and a heterocercal tail fin. Global distribution, Silurian to Carboniferous.

Climatius a primitive genus of acanthodian fish in the family Climatiidae. Although only about 3 inches long, it had the typical large shoulder girdle of acanthodians and a total of 15 spines on its body and fins. *Climatius* is well-known in several species from across North America and Europe; the best known is *C. reticulatus*, the type species. Late Silurian to Early Devonian.

Cloudina a genus of Ediacaran fossils found as a tube with nesting conical shells and double-layered walls of calcium carbonate. Generally thought to have been made by a suspension-feeding worm, it was one of the earliest-known shelled organism. See also ***Namacalathus***. Its shells typically show signs of predation. Named for American paleontologist Preston Cloud, *Cloudina* was first found in Namibia but is now known worldwide; late Ediacaran to Cambrian.

Clubionidae the sac spiders, a family of araneomorph spiders in the superfamily Araneoidea; global distribution, late Eocene to Recent.

Clydoniceras discus a genus of small ammonoids. Important stratigraphically in the Bathonian, it was 2–3 inches in diameter and relatively smooth-shelled with a goniatitic suture line. Europe and Saudi Arabia, Middle Jurassic, 167 Ma.

Clymeniida a large early order of ammonoids, notable for an unusual dorsal siphuncle, as opposed to the ventral siphuncle of other ammonoids. Less than 2 inches in diameter and very diverse in shell type and ornamentation, they diversified rapidly in the Famennian, the final age of the Devonian, but then abruptly disappeared at the end of the period. Europe, North Africa, and possibly Australia; Middle to Late Devonian.

Clypeasteroida the sand dollars, an order of irregular euechinoids. Their ancestors diverged from other irregular echinoids in the Jurassic. Global distribution, late Paleocene to Recent.

Clypeus ploti "swimming shield," a species of irregular echinoids in the family Clypeidae, called the "pound-stone" because it fossilized as a rounded, fist-sized stone of about 20 ounces. Common in the eighteenth-century Oxfordshire, England, it was among the first echinoids studied. Europe and Africa, Middle Jurassic.

Cnidaria a phylum of diploblastic animals, mostly marine, usually with stinging tentacles around the mouth. Comprising chiefly the corals, sea anemones, jellyfish, and hydrozoans, the phylum includes more than 10,000 named species, divided into three classes: **Anthozoa** (corals and sea anemones)**, Scyphozoa** (the jellyfish), and **Hydrozoa**, *q.v*. The early Cnidaria were especially significant in developing discrete tissues for various body functions, a significant evolutionary advance beyond the sponges. Ediacaran to Recent.

Coccolithophore a type of one-celled planktic algae that surrounds itself with a many-layered calcite skeleton (a coccosphere). The skeletons are the major component of chalk deposits around the world, and coccolithophores are considered the main calcite producer in the ocean. Coccolithophores are significant in the fossil record since the Triassic, especially as an indicator of climate change.

Coccosteus an important Devonian genus of arthrodire placoderms in the suborder Brachythoraci. Similar in some ways to its much larger cousin *Dunkleosteus*, *Coccosteus* was 8 to 16 inches long and is found mainly in freshwater deposits. It had large pectoral and pelvic fins and a long, finned tail. The arthrodires were joint-necked fish, and *Coccosteus* had two joints which allowed it to feed on large prey. Europe and North America, Middle to Late Devonian.

Cochliodontidae a large family of elasmobranch fish similar to sharks but with a bradyodont toothplate dentition; Devonian to Permian.

Codaster a genus of blastoid echinoderms in the order Fissiculata and family Codasteridae. Generally just under 1 inch long, it had a unique shape, pentameral and rounded at the top but pointed at the bottom. Like other blastoids, it was attached to the substrate by a stem. United States and Kazakhstan, Silurian to Pennsylvanian.

Coelacanthidae an extinct family of actinistian lobe-fin fish in the order Coelacanthiformes; Permian to Jurassic.

Coelacanthiformes an order of lobe-fin fish, considered extinct since the Cretaceous until two species of the genus *Latimeria* were discovered in the Indian Ocean in 1938. *Latimeria* (Latimerioidei: Latimeriidae), which appeared in the Triassic, is very similar to the Cretaceous coelacanths. Even with a poor fossil record, coelacanths are significant in evolution because they are closely related to the early lobe-finned fish, which are thought to be the first fish to develop air-breathing skills that let them begin to live on land about 400 Ma. Devonian to Recent.

Coelenterata an obsolete term. Coelenterata were formerly considered a phylum that included a large group, the Cnidaria, and a smaller group, the Ctenophora; these are now considered separate phyla.

Coelodonta a genus of large perissodactyl mammals in the extant suborder Ceratomorpha and subfamily Rhinoceratinae. Coelodonts were the wooly rhinoceroses of Eurasia, surviving up to about 10,000 years ago. Similar in size to the modern rhinoceros, typically about 13 feet long and weighing 3 tons, with some almost 7 feet high, they bore two forward-pointing horns on the nose. Europe and Asia, Pliocene to late Pleistocene.

Coelom a body cavity, lined with mesodermal tissue, within which the organs can develop.

Coelophysis a genus of early saurischian dinosaurs, theropods in the family Coelophysidae. Bipedal, lightly built, and about 10 feet long, it is a typical coelurosaur. There is some inconclusive evidence that it was gregarious, perhaps hunting in packs. United States, Late Triassic to Early Jurassic.

Coeloria a genus of scleractinian corals; synonym *Platygyra. Coeloria* is notable for its long, meandering corallites that form striking labyrinthine patterns on the surface of the colony. Global distribution, Paleocene to Recent.

Coelosmilia a genus of scleractinian corals in the family Caryophylliidae; synonym *Anomocora*. *Coelosmilia* is the only purely calcitic genus of the normally aragonitic Scleractinia. Possibly indicating a low ratio of magnesium to calcium in the ocean, it is important in describing the chemical composition of Mesozoic oceans. Europe, North America, and India; Middle Jurassic to Paleocene, 168–62 Ma.

Coelurosauravus see **Weigeltisauridae**.

Coelurosauria a large group of small, lightly built, theropod dinosaurs, generally considered saurischians. These bipedal predators, most of them feathered, became prominent in the Middle Jurassic and gave rise to later saurischians such as the Compsognathidae, Ornithomimidae, and Tyrannosauridae and to birds. Triassic to Late Cretaceous.

Coenopteridales a large and varied group of ancestral ferns, usually considered as belonging to the order Primofilices; Devonian to Triassic.

Coevolution an evolutionary process in which unrelated lineages exert selective pressure on each other, resulting in evolutionary changes in both. The best-documented cases are the interactions between insects and entomophilous and entomophagous flowers and between birds and ornithophilous flowers, but many other cases have been described of coevolutionary relationships between predatory animals and prey and between herbivorous animals and plants.

Coleodontidae a family of conodonts in the order Neurodontiformes, with lamellar teeth; Ordovician to Triassic.

Coleoidea a subclass of mostly soft-bodied mollusks in the class Cephalopoda, including the extinct belemnites and the extant squids, octopuses, cuttlefish, and the Spirulida. Disputed coleoids are known from as early as the Cambrian, but the earliest definitive coleoids are dated as Mississippian.

Coleoptera the beetles, an order of pterygote insects in the clade Neoptera. They are named "sheathed wing" for the hard elytra, the front pair of wings that protect the membranous back wings and the abdomen. The oldest definitive beetle dates back to the Permian, but a possible specimen has been found at the Late Carboniferous Mazon Creek site. Following the end-Permian extinction, the Coleoptera diversified rapidly in the Triassic. Global distribution, Pennsylvanian? to Recent.

Collembola an extant order of primitive apterygote hexapods in the class Entognatha, probably the first terrestrial animals. Up to half a centimeter long, they are commonly called springtails because of the jumping ability given them by a furcula, a taillike forked appendage at the end of the abdomen and normally folded under the body. Known from the Early Devonian *Rhyniella praecursor* and other fossil specimens beginning in the Cretaceous.

Collenia a genus of Proterozoic cyanobacteria that produced stromatolites with slightly convex layers of microbial mats. Its columnar colonies are known mainly from Minnesota and Montana. United States, early Proterozoic, 2400–2100 Ma.

Collignoniceras a small genus of ammonoids in the order Ammonitida and superfamily Acanthoceratoidea. Up to 7 inches in diameter, evolute, and very strongly ribbed, *Collignoniceras* is the type genus of the family Collignoniceratidae. Global distribution, Late Cretaceous, 96–88 Ma.

Collinsium ciliosum see ***Hallucigenia*.**

Collyrites a genus of small irregular euechinoids in the family Collyritidae, possibly paraphyletic. They were oval, up to an inch long, and did not have a lantern. Europe and Asia, Middle Jurassic to Early Cretaceous.

Colobops noviportensis a species of small archosauromorph reptiles, tentatively placed in the order Rhynchosauria but possibly rhynchocephalian. Poorly known, only from a 1 inch skull found in the New Haven Arkose Formation (which provides its species name), it is estimated at 6–8 inches long. The skull's structure and attachments indicate that it had large jaw muscles that would give it a more powerful bite than other small reptiles of the time. United States, Late Triassic.

Columba omnisanctorum an extinct species of early Pliocene pigeons in the order Columbiformes. It is known only from the Gargano Peninsula of Italy and is related to a similar columbiform found nearby, *C. pisana*. See also ***Deinogalerix***.

Columbia see **Rodinia**.

Colymbosathon ecplecticos a species of ostracods notable for the well-preserved soft-tissue features in one intact specimen buried by volcanic ash about 425 Ma and found in a carbonate nodule. Although the fossil is only 0.2 inches long, organs

visible in a digital three-dimensional image include eyes, gills, a circulatory system, anus, and penis. The presence of the penis makes this specimen the earliest-known definitively male fossil. See **Herefordshire Nodules**. England, Silurian.

Comatulida a large order of articulate crinoids that appeared in the Triassic, flourished in the Jurassic and Cretaceous, and is now the dominant extant group of crinoids. Most comatulids (the feather stars) are free-living, generally sedentary but unstalked as adults, attaching to the substrate by means of hook-shaped cirri as they move from place to place. A few comatulids retain their stalk and may be seen as distinct from the feather stars. Global distribution, Triassic to Recent.

Comb jellies see **Ctenophora**.

Commensal referring to a relationship between two organisms in which one partner benefits without significantly affecting the other.

Como Bluff a Konzentrat-Lagerstätte on a ridge in Wyoming noted for the many dinosaurs discovered there in strata of the Morrison and Sundance Formations; United States, Middle and Late Jurassic.

Composita a large genus of articulate rhynchonellate brachiopods in the order Athyridida. Biconvex, it is from 1 to 2 inches in diameter and is smooth-shelled with fine growth lines. It has a fold, a sulcus, and a round pedicle aperture. Global distribution, Late Devonian to Early Triassic.

Compositae (angiosperm): see **Asteraceae.**

Compound eye an eye formed of a mosaic of smaller eyes, characteristic of many arthropods.

Compsemys a monospecific genus of cryptodire turtles in the family Compsemydidae. *C. victa* was 1 foot long, and its carapace bears many raised tubercles, distinguishing it from other turtles. North America, Early Cretaceous to late Paleocene.

Compsognathus "dainty jaw," a genus of theropod saurischian dinosaurs in the family Compsognathidae. Known from two almost complete skeletons from France and Germany, it was birdlike and very light in build, as long as 4 feet but weighing only about 8 pounds. A fast runner, it had long hind legs and a long tail. Europe, Late Jurassic, 150 Ma.

Concestor see **MRCA**.

Conchostraca see **Branchiopoda**.

Concretions hard, layered structures, usually rounded, embedded in rock of a different kind, formed by precipitation and cementation of minerals in the soil or rock around a nucleus, sometimes enclosing a fossil.

Condylarths an informal group of primitive placental mammals ancestral to the perissodactyl ungulates and to the cetaceans. Previously considered an order, the condylarths have all been reassigned more precisely to different orders. Arising in the Cretaceous, they underwent an extensive radiation of species in the Paleocene and Eocene. They were mainly herbivorous, but some had hooves and some had claws. Global distribution except Australia, Late Cretaceous to Oligocene.

Condyle an articular process, a pivot point, on the joint of a bone (or mandible of an insect).

Confuciusornis a genus of primitive birds in the family Confuciusornithidae, of which *C. sanctus* is the type species. Crow-sized, it is the earliest-known toothless beaked bird and seems to be one of the earliest that could fly for a considerable distance. It did not, however, have an alula, which would have improved its maneuverability. (See ***Eoalulavis*** and ***Protopteryx***.) About 11 inches high and bearing true feathers, it was similar to *Archaeopteryx* except that it was toothless and probably had more feathers. Three other species have been named, all found in the Yixian and Jiufotang Formations of Northeastern China (see **Jehol Biota**) and dated between 130 and 125 Ma, 10–15 million years after *Archaeopteryx*. *Confuciusornis* was probably not in the line of descent to modern birds. China, Early Cretaceous.

Coniconchia a proposed class of mollusks to include the hyoliths and tentaculites. Research in 2017, however, indicates the hyoliths are lophophorates and closely related to brachiopods. The tentaculites are generally considered an order in their own right, the Tentaculitida. See also **Cornulitida**.

Conidae a very large extant family of cone snails, marine gastropod mollusks in the superfamily Conoidea. They are generally 1–3 inches long but may grow to as much as 9 inches. The shells are conical, generally with a flattened cone-shape at the large end; the smaller end is acutely conical and has a long, narrow aperture. Global distribution, Early Cretaceous to Recent.

Conifers see **Pinopsida**.

Coniophis a genus of snakes in the clade Ophidia and suborder Serpentes. Only 3 inches long and one of the earliest-known snakes, *Coniophis* is known primarily from a set of fragile bones found in Montana and Wyoming, although other fragmentary and questionable remains have been found in Africa, Asia, and South America. Its date is also in question, given variously between 94 and 34 Ma. Cosmopolitan, Late Cretaceous,

Coniopteris a genus of Mesozoic ferns in the extant family Dicksoniaceae. It bore lanceolate or lobate leaves 2–4 inches wide, which carried the spores marginally, in cup-shaped pouches at the end of lateral veins. Global distribution, Permian to Cretaceous; especially common in the Jurassic.

Conocardium a genus of rostroconch mollusks in the family Conocardiidae. Up to 6 inches long, its thick, unequal valves had a long, straight hinge line and a surface marked by fine rays. Global distribution, Devonian to Permian.

Conoclypus a genus of euechinoids in the order Clypeasteroida and family Conoclypidae, sand dollars with a high, conical test 2–4 inches in diameter; Europe, early Eocene to Miocene.

Conocoryphe a genus of trilobites in the order Ptychopariida. Very similar to ***Ptychoparia,*** *q.v.*, except for generally being eyeless; one species, *C. oculata*, had small eyes and at least some vision. Europe and United States, middle Cambrian.

Cono-cylindrical a common shape in many rugose corals, basically conical but slender and cylindrical in part of its length.

Conodonta a class of enigmatic eellike chordates. Although considered vertebrates, they are still known mainly by their feeding apparatus, referred to as conodont elements; fossil specimens show no soft-tissue detail. Their jaw structure differs greatly from that of later animals. They are now classified as chordates and divided into protoconodonts, paraconodonts, and euconodonts. Appearing in the early Cambrian, they ranged from an inch to more than a foot long. Only a few whole-body specimens have been found, the best known of which is ***Promissum pulchrum,*** *q.v.* Since they evolved rapidly, most species were short-lived, so that they are very useful stratigraphically. Many conodonts became extinct at the end of the Ordovician, but they recovered and continued to be important through the Paleozoic, becoming completely extinct at the end of the Triassic.

Conodont elements the earliest tooth fossils, in the form of rudimentary teeth and very rudimentary jaws. Despite the inability until recently to discover whole-body specimens of the animal which bore them, conodont elements have long been important in stratigraphic research. See, for example, ***Iapetognathus*** and ***Streptognathodus***.

Conophyton one of many plantlike organisms that formed stromatolites in the Mesoproterozoic Era; North America and Africa, Archaean.

Constellaria a genus of stenolaemate bryozoans in the extinct order Cystoporata and family Constellariidae. They formed branching colonies and are distinguished by generally star-shaped maculae, about half an inch across, on the surface of branches. Global distribution, Middle Ordovician to early Silurian.

Continental drift see **paleogeography**.

Conulariida a problematic clade of cnidarians, generally considered scyphozoans but not well understood; synonyms: Conulata and Conularia. Their superficially shell-like structure, up to 6 inches long, consists of rows of calcium phosphate rods that form a quadrilateral cone, with new rods added at the broader end. The surface has a wavy ridged appearance, with the rows of rods intersecting at a slight angle in the middle of each side. The narrow end was attached to the substrate, and soft tentacles extended from the broad end. The larger conulariids were as long as 20 inches, but most were about 4 inches. Late Cambrian to Jurassic.

Conulidea a superfamily of echinoids in the order Echinoneoida; Europe, Asia, and North America; Early Cretaceous to Eocene.

Conulus a small genus of euechinoids in the order Echinoneoida and family Conulidae. It was dorsally high-domed, almost conical, smooth, and nonpetaloid; the flat oral side has a faint pentameral pattern. Europe, Asia, North America; Early to Late Cretaceous.

Convergent evolution the process in which unrelated lineages living in similar environments independently develop superficially similar but nonhomologous adaptations; for prominent examples, see **bivalves**, ***Thylacosmilus***, and **Xenarthra**.

Cooksonia a transitional genus of tracheophytic plants in the family Rhyniaceae. Only a few inches high, it was a simple branching plant, the oldest demonstrably vascular plant; it lived close to the time when the lycopsids branched off from other plants. Global distribution, middle Silurian to Early Devonian.

Cope's rule the name given to the observation that groups of animals tend to evolve toward larger size over evolutionary time. The idea is associated with the nineteenth-century paleontologist Edward Drinker Cope and has been elaborated by many others. The tendency is obvious in many lineages but absent in others and of course must be subject to limitations of sufficient food sources and of the ability to move efficiently. See also **Unspecialized Descent**.

Copodus a little-known genus of primitive holocephalic fish in the extinct family Copodontidae. Its dentition was bradyodont, with one toothplate in each jaw. North America and Europe, Devonian and Carboniferous.

Coprolites fossilized residues from the digestive tracts of animals. Their contents may provide evidence of the existence of other organisms, and they are important in investigating eating habits of animals, but it is difficult to identify the producer. The largest-known specimen is about 17 inches long, found in Saskatchewan in 1995 and thought to have come from a large tyrannosaur just before the end of the Mesozoic era. Usually in the form of dung, coprolites may also be regurgitalites (regurgitated) or cololites (fossilized inside the body).

Corallite the chamber or skeleton constructed by an individual coral polyp.

Corallum the skeleton of an entire coral colony, consisting of many individual corallites.

Corals see **Anthozoa**.

Cordaicarpus the form genus of seeds of the family Cordaitaceae.

Cordaitales an order of primitive gymnosperm plants in the class Pinopsida. Possibly ancestral to conifers, cycads, and ginkgos, they were treelike, growing as high as 100 feet with long, strap-like leaves. Global distribution, Carboniferous to Late Triassic.

Cornulitida a proposed order of small encrusting tubeworms of the middle Paleozoic. Similar to the microconchids but less euryhaline, they are now generally placed with tentaculitids; others have considered them trypanoporids. Found worldwide in normally saline oceans, they constructed a straight, slightly conical tube less than an inch long, often with strongly ribbed annulations. Cornulitids are typically found in their life position on organisms like brachiopods or on other hard substrate surfaces. They appeared in the Ordovician, flourished from the Late Ordovician to the Early Devonian, and declined until becoming extinct by the middle of the Carboniferous.

Cornupalpatum a genus of hard ticks in the family Ixodidae, known from several specimens in amber; Burma, Late Cretaceous, 99 Ma.

Coronacollina the earliest-known animal with skeletal body parts, possibly related to sponges. A genus of benthic organisms 1–2 inches high, with 3 spicules radiating from a central thimble-shaped body; the long spicules probably supported the animal on the ocean floor. Its resemblance to the Cambrian sponge *Choia* indicates a link between the two periods. Described in 2012 from hundreds of specimens found in upper Ediacaran strata in Australia, 560–550 Ma.

Coronodon havensteini a species of mysticete whales known only from a large, complete skull with unusual dentition. It has strikingly ridged molar teeth that show no wear from cutting and shearing prey, leading some to consider *Coronodon* evidence of a transition from the toothed condition of the early odontocete whales to the baleen of the mysticetes. The very large molars, 3–4 inches in diameter, might have sieved food from the water as baleen does in modern mysticetes; however, this interpretation is in dispute. United States, early Oligocene.

Correlated progression model an evolutionary hypothesis suggested as a refinement of the concept of modular or mosaic evolution. It is usually stated thus: evolutionary change of characters occurs by a correlated response, so that a change in one

character may influence change in another. Its main proponent, T.S. Kemp, states that it is "a systems-related concept … in which all the traits are functionally linked and so constrained to evolve by small increments at a time in parallel with each other."

Corynexochida a diverse order of early trilobites that appeared at about the same time as the Ptychopariida, probably descended from the Redlichiida. The Corynexochida generally have large eyes and a large glabella extending nearly to the front of the cephalon. Global distribution, early Cambrian to Middle or Late Devonian.

Coryphodontidae a family of pantodont mammals in the extinct order Cimolesta. The type genus *Coryphodon* was 3 feet at the shoulder and about 8 feet long, and some genera were larger. Although the canine teeth were relatively long, they were forest browsers. North America, Europe, and Asia; late Paleocene to middle Eocene.

Corystospermaceae a family of seed ferns in the division Pteridospermatophyta and order Peltaspermales. They bore pairs of heavily veined leaflets on a central stalk. Widespread in the Triassic throughout Gondwana and present also at least in China; Early to Late Triassic.

Corythoraptor jacobsi a species of feathered theropod dinosaurs in the family Oviraptoridae, known from one almost complete skeleton. Described in 2017, *C. jacobsi* was 5–6 feet long, with small forelimbs and strong hindlimbs, probably flightless but a fast runner. In shape it resembled the modern cassowary, especially because of a tall, characteristic crest. It is one of several oviraptoroids found in the Nanxiong Formation; Southern China, Late Cretaceous, 84–66 Ma.

Corythosaurus a genus of hadrosaurid dinosaurs in the subfamily Lambeosaurinae. Similar to *Lambeosaurus*, it was about 30 feet long, with a stocky body and long tail. Its most notable feature was a tall, rounded crest on the top of its head; see also ***Parasaurolophus***. North America, Late Cretaceous, 80–74 Ma.

Cosmopolitan distribution existing in appropriate but scattered environments across all or most of the world.

Cotylorhynchus a genus of synapsids in the family Caseidae; it was 10–12 feet long, with a large, barrel-shaped body and a very small head. The type species *C. romeri* was widespread in the southern part of North America in the early Permian. North America, Carboniferous to middle Permian.

Cotylosaurs an informal term for the paraphyletic Captorhinida.

Craniate having a specialized and distinctly formed head, distinguishing most chordates from tunicates and cephalochordates.

Craniiformea a subphylum of inarticulate brachiopods that includes the class Craniforma and three orders: the extant Craniida and the extinct Craniopsida and Trimerellida. The Craniiformea have an unsupported lophophore and no pedicle; the calcitic ventral valve is generally found cemented to the substrate or to another brachiopod. Early Ordovician to Recent.

Craniopsida an order of inarticulate brachiopods in the class Craniforma. One of the earliest groups of brachiopods, they share some features with the enigmatic Kirengellidae. Global distribution, early Cambrian to Early Carboniferous, 516–343 Ma.

Crassatella a long-lived genus of articulate marine burrowing bivalves. *Crassatella* was 1.5 inches long, with a strong shoulder on both shells and strong concentric growth lines. Cretaceous to Recent.

Crato Formation a Lower Cretaceous Konzentrat-Lagerstätte in the Araripe Basin of Northern Brazil, dated uncertainly but probably between 115 and 112 Ma, slightly earlier than the neighboring Santana Formation. The occurrence of the Crato fossils differs from that of the Santana fossils, which are found in limestone concretions. Those of the Crato, found in finely bedded limestone similar to that of Solnhofen, are predominantly arthropods, especially insects and arachnids, with some specimens of fish such as *Dastilbe* and crested pterosaurs such as *Anhanguera*. There are other vertebrates and a variety of plants including gymnosperms and other early seed plants, as well as a few angiosperms.

Craugastor an extant genus of tree frogs known from amber fossils found in the Dominican Republic and Mexico, about half an inch long; late Oligocene to Recent.

Creodonts an informal term for a polyphyletic group of flesh-eating mammals formerly considered an order, including the Oxyaenidae and Hyaenodontidae; the origins of the group are unclear. The diverse group included carnivores as small as squirrels and as large as bears. North America, Europe, Asia, and Africa; Late Cretaceous to Miocene.

Crepidula an extant genus of marine mollusks, prosobranch gastropods in the family Calyptraeidae, commonly called slipper snails. Medium-sized and low-spired, *Crepidula* has a prominent, twisted beak and typically has a platform covering half of the large aperture. Global distribution, Early Cretaceous to Recent.

Crepiporinae see **Ceramoporidae**.

Cretaceous the third and final period of the Mesozoic Era, from 146 to 66.0 Ma, divided into Early (146–100) and Late (100–66.0) Epochs. It was a period of high levels of carbon dioxide, very little polar ice, and the highest sea levels in Earth's history, with shallow, saline seas covering much of the land. Dinosaurs continued

their reign on land, and marine life was dominated by the greatly diversified bony fish and large predators such as sharks and mosasaurs.

The first angiosperms appeared early in the period and by the end of the Cretaceous were the dominant plants worldwide, replacing the declining cycads, ginkgophytes, and Mesozoic pteridosperms. The cycadeoids reached extinction at the end of the period. Insects and spiders diversified rapidly along with the angiosperms.

Cretaceous extinction the most recent and second-most severe of the five great extinctions, ending the Mesozoic Era at about 66.0 Ma; the end of the era is often referred to as the K-T boundary. The most striking result for animal life was the disappearance of the last of the dinosaurs and pterosaurs, and other large animals were also decimated, so that the largest that survived into the Paleocene was about the size of a turkey. An interesting side note is that frogs and salamanders seem to have survived in greater numbers than other land animals, at least in well-studied sites of the Hell Creek Formation in Montana that straddle the K-T boundary. In the seas, the last of the ammonoids and other groups became extinct, as well as the plesiosaurs and mosasaurs.

As to possible causes, the preponderance of evidence points to a large asteroid, referred to as the Chicxulub asteroid, striking the Earth off the Yucatan Peninsula and causing global environmental disruption, and the volcanic eruption creating the basalt flows called the Deccan Traps in India may have contributed; but, as with the four earlier mass extinctions, the causes are uncertain. Although the number of dinosaur species decreased during the last several million years of the Cretaceous, the evidence for a relatively abrupt extinction event is stronger than in the other mass extinctions.

Cretaceous Inland Seaway see **Western Interior Seaway**.

Cretaceous Terrestrial Revolution abbreviated as KTR, the period of angiosperm radiation from 125 to 90 Ma, when flowering plants, insects, and spiders radiated dramatically, leading to an accompanying radiation of many other animals.

Cretaraneus a genus of araneomorph spiders in the family Nephilidae. An orb-weaver, *Cretaraneus* is well-known in many specimens from the Crato Lagerstätte of Brazil and also from Spain and China. Early Cretaceous, 130–112 Ma.

Cretoxyrhinidae an extinct family of very large Cretaceous sharks in the extant order Lamniformes. Up to 23 feet long and bearing very sharp 3-inch-long teeth, they preyed on mosasaurs, bony fish, and turtles. Cosmopolitan, Late Cretaceous, 94–70 Ma.

Cribellum a platelike silk-spinning organ of cribellate spiders which produces extremely fine silk through many small pores. The cribellum is a relatively primitive feature: most modern spiders produce silk through elongate spinnerets.

Crinoidea a class of marine crinozoan echinoderms, commonly called "sea lilies." Crinoidea is generally taken to include three subclasses: Articulata, Flexibilia, Camerata; a 2017 study classifies only two subclasses, Camerata and Pentacrinoidea, considering Articulata and Flexibilia as superorders.

Crinoids are generally sessile and have, like all echinoderms, pentameral symmetry. They have a cup-shaped body surrounded by a circlet of plates extending into a cluster of arms. Their mouth, however, unlike most echinoderms, is directed upward. Stalked, unstalked, and free-swimming genera are known, but the classic Paleozoic genera were stalked. The columnal stems are composed of a series of plates, which are often found singly. Stems are generally circular but also often pentagonal or star-shaped and sometimes even elliptical. About 7000 extinct species are known, with the greatest diversity in the Paleozoic. They may have arisen from the Edrioasteroidea or from the eocrinoids and their descendants the cystoids.

Crinoids were widespread and numerous throughout the Paleozoic up to the end-Permian extinction, and many Paleozoic limestones consist almost wholly of crinoid fragments. The Camerata, Flexibilia, and most other groups became extinct at the end of the Permian; the survivors into the Early Triassic are still widely disputed (see **Ampelocrinidae**), but the Articulata originated either in the late Permian or Early Triassic and are the principal extant group. Except for the Articulata, the crinoids declined rapidly in the Mesozoic for poorly understood reasons, leaving 100 extant genera and 600 extant species at present. See also **Bobcaygeon**. Early Ordovician to Recent.

Crinozoa a subphylum of echinoderms generally considered to include the class Crinoidea and the extinct classes Cystoidea, Edrioasteroidea, and Paracrinoidea.

Crocodylia an extant order of predatory, semiaquatic reptiles; global distribution, Late Cretaceous to Recent.

Crocodylomorpha a large superorder of archosaurs that includes the crocodilians and their extinct relatives, going back to the sphenosuchians of the Late Triassic; global distribution, Late Triassic to Recent.

Cro-Magnon the common name for the hominins who competed with Neanderthals in Europe after 40,000 years ago. Now referred to as "European early modern humans," the Cro-Magnons are classified in the same subspecies as modern humans, *H. sapiens sapiens*, because the skeletal differences between the two are insignificant.

Crossopterygii see **Sarcopterygii**.

Crown group a monophyletic group comprised of a set of extant species, together with their ancestors back to their latest common ancestor and all other descendants of that common ancestor; see also **stem group.**

Crustacea a large subphylum of arthropods that includes crabs, lobsters, shrimp, krill, barnacles, ostracods, branchiopods, and other similar animals; middle Cambrian to Recent.

Cryogenian Glaciation A period of global cooling around 650 Ma; see **acritarchs** and **icehouse conditions**.

Cryolophosaurus a genus of early theropod dinosaurs found in the Hanson Formation in Antarctica in 1991. It is probably tetanuran but has some dilophosaurid features, distinctively a thin bony crest across the top of its forehead. Weighing half a ton and about 21 feet long, *Cryolophosaurus* had a shallow skull and a long, stiff tail. It is known only from an immature specimen, but it was one of the largest theropods of its time and was probably an efficient predator. Antarctica, Early Jurassic, 190 Ma.

Cryptoclidus "hidden collar bone," a genus of plesiosaurs in the family Cryptoclididae. About 13 feet long with a short tail and four strong flippers, *Cryptoclidus* closely resembles its later relative, *Plesiosaurus*. Europe, Asia, and South America; Middle Jurassic, 166–164 Ma.

Cryptodira an extant suborder of turtles in the order Testudines, including most of the modern turtles and tortoises. They differ from the Pleurodira in several ways, notably by retracting the head inside the shell by vertical flexure, directly back instead of to the side. They evolved along with the pleurodires in the Early Jurassic and by the end of the period had largely replaced them. Global distribution except Australia, Early Jurassic to Recent.

Cryptograptus a genus of scandent pterobranch-like graptolites in the suborder Glossograptina; cosmopolitan, Middle Ordovician to late Silurian.

Cryptolithus a genus of asaphid trilobites in the family Trinucleidae. Almost circular in shape and eyeless, but with a pitted fringe around its head that may have allowed it to sense the direction of ocean currents as it fed on small animals in ocean sediments. In addition to this "lace collar," *Cryptolithus* was remarkable for its pair of long genal spines. It became extinct in the Ashgill event, 440 Ma. Cosmopolitan, Late Ordovician.

Cryptostomata an order of Paleozoic colonial bryozoans in the extant class Stenolaemata. The zoaria are short but erect, and the colony forms bifurcating branches. Ordovician to Permian.

Cryptovolans see ***Microraptor*.**

Cryptozoon an enigmatic genus of stromatolitic reef-forming algae common in the Cambrian and Ordovician, possibly extant in the stromatolites of Shark Bay, Australia.

Ctenodactylidae an extant family of rodents in the suborder Hystricomorpha, named for the stiff bristles on their hind feet. The earliest definitive specimen is from the late Eocene, but DNA evidence indicates that the first Ctenodactylidae appeared in the early Eocene in Asia. The family is still represented by several pika-like North African genera, called gundis, which are commonly called "comb-rats." Asia, Europe, and Africa; Eocene to Recent.

Ctenodonta a genus of burrowing protobranch bivalve mollusks in the order Solemyida and family Ctenodontidae. About an inch long, it was equivalved and had numerous teeth at the hinge line. The shell was either smooth or marked with fine, concentric growth lines. Global distribution, Early Ordovician to Carboniferous.

Ctenodus "comb-tooth," a genus of sarcopterygian fish in the order Dipnoi, ancestral to the modern lungfishes in a well-documented evolutionary line; North America, Europe, and Australia; Early Carboniferous.

Ctenoid scales comb-like fish scales that have a rough edge, with many small projections.

Ctenophora the comb jellies, a phylum of gelatinous marine animals that move by the beating motion of their cilia. Generally bell- or ribbon-shaped, they are hermaphroditic and predatory, feeding on zooplankton and fish larvae. Global distribution, early Cambrian to Recent.

Ctenothrissiformes a small order of teleost fish in the subclass Neopterygii, well-known from the genera *Ctenothrissa* and *Aulolepis*. Appearing only in the Cenomanian Age of the Late Cretaceous, they seem to be close to the ancestry of most modern bony fish. They were deep-bodied and about a foot long, characterized by ctenoid scales and large dorsal and pectoral fins without true spines. Europe and Southwest Asia, Late Cretaceous, 95–90 Ma.

Ctenurella "small tail comb," a genus of benthic ptyctodontid placoderm fish. About 5 inches long, it was lightly armored, like the other ptyctodontids. It had a whiplike tail and two dorsal fins, the one near the tail comb-shaped, long and low. It had small toothplates and was probably viviparous. Germany and Australia, Late Devonian.

Cursorial of terrestrial animals, adapted to rapid running movement in open country.

Cuvieronius a genus of New-World proboscideans in the extinct family Gomphotheriidae. A small gomphothere, *Cuvieronius* (also known as *Cordillerion*) was 9 feet high, weighed about 4 tons, and was notable for its two spirally twisted tusks. It lived in North America from the Pliocene up to the end of the Pleistocene and in South America until about 9000 years ago, the latest specimen being found in Chile. Pliocene to Holocene.

Cyanobacteria see **Cyanophyta**.

Cyanophyta a phylum of bacteria, one of the earliest forms of life on Earth, found in Precambrian deposits as old as 3 billion years. They are also called cyanobacteria and "blue-green algae," although not algae at all. Since they produce oxygen through photosynthesis, they may have significantly changed the composition of the atmosphere as they spread worldwide.

Cyathaspidiformes an order of jawless heterostracan fish, the second-largest group of heterostracans. Fusiform and heavily armored, they were all benthic. Middle Ordovician to Middle Devonian.

Cybele a genus of phacopid trilobites in the family Encrinuridae. About 2 inches long, it had a small glabella with eyestalks, a long thorax, and trailing pleural spines. It probably hunted from ambush, covered with seafloor detritus. Europe and North America, Early to late Ordovician.

Cycadales one of the two orders of the Cycadopsida, the Cycadales include the living cycads and their immediate ancestors. They are subtropical plants with large, stiff, fernlike leaves, forming a crown around the top of the stem. Cycads are gymnosperms and are not related to palms, which are angiosperms; early Permian to Recent.

Cycadeoidales the second order of treelike plants in the Cycadopsida. The Cycadeoidales include the many extinct cycad-like plants that were widespread, along with the true cycads, throughout the Mesozoic. Permian to Cretaceous.

Cycadofilicales see **Pteridospermatophyta**.

Cycadopsida the class of early seed plants that includes principally the cycads; early Permian to Recent.

Cyclacantharia a genus of strophomenate brachiopods in the order Productida, variously placed in the families Richthofeniidae or Cyclacanthariidae. Characterized by a large conical valve cemented to the substrate with many prop-like spines, it is an aberrant form. It is known especially from specimens found in the Glass Mountains of Texas, with the calcite shell replaced by silicification. United States, Africa, and Asia; early to late Permian.

Cyclestherida see **Branchiopoda**.

Cyclida an enigmatic order of arthropods, formerly considered crustaceans but now classified as maxillopod branchiurans, related to modern fish-lice. Originally called Cycloidea, they were crab-shaped with a circular carapace 1–2 inches in diameter. A dozen genera are recognized, including *Apionicon*, *Carcinaspides*, *Halicyne*, and *Hemitrochiscus*. Europe and North America, Carboniferous to Late Cretaceous.

Cyclocystoidea a small middle Paleozoic class of echinoderms in the subphylum Echinozoa, formerly placed in the class Edrioasteroidea. They are small and disc-shaped and had a marginal ring of ossicles around a plated disc. North America and Europe, Middle Ordovician to Early Carboniferous.

Cycloidea see **Cyclida**.

Cyclomedusa a very contentious fossil widespread in the Ediacaran biota, possibly related to *Aspidella*. Circular and up to 10 inches in diameter, it is generally flat, with many concentric growth ridges, and some specimens display fine radial lines and possible stems. It is variously considered a holdfast, possibly from an octocoral-like organism; a colonial microbial organism; or an anemone-like benthic polyp. Global distribution, Ediacaran.

Cyclopyge a genus of small asaphid trilobites in the family Cyclopygidae. The cephalon was massive, with large, convex holochroal eyes to the sides of a large, domed glabella. Its thorax was relatively short, with only 6–7 segments. Europe, North Africa, North America, and Asia; Early to Late Ordovician.

Cyclopygidae a family of small- to medium-sized trilobites in the order Asaphida. They had very large holochroal eyes and are found mainly in deep-ocean sediments, probably pelagic and often swimming upside down. The principal genera are *Cyclopyge, Pricyclopyge,* and *Symphysops*. Along with many other groups of trilobites, they became extinct at the end of the Ordovician. Global distribution, Early to Late Ordovician.

Cyclostomata an extant group of jawless fish that includes the lampreys and hagfishes. Whether it should be considered a class of agnathans or a separate superclass is debatable. Global distribution, Early Devonian to Recent.

Cyclostomatida an extant order of bryozoans in the class Stenolaemata; synonym Tubuliporata. They were the predominant bryozoans in the Mesozoic and have declined since then but are still widespread. Not to be confused with the Cyclostomata, the lampreys, and hagfishes. Early Ordovician to Recent.

Cyclothyris an obscure extinct genus of articulate brachiopods in the extant order Rhynchonellida. It had a subtriangular shape and an erect beak. Cosmopolitan, Cretaceous.

Cymbiocrinidae a contentious family of crinoids usually placed in the order Cladida, sometimes mentioned as a possible stem group of the class Articulata. United States and Australia, Early to Late Carboniferous.

Cymbionites a genus of small echinoderms in the class Eocrinoidea. Poorly known, *Cymbionites* is thought to be the basal circlet of an eocrinoid. It was about half an inch across, bowl-shaped and composed of five plates. Australia, early Cambrian, 515 Ma.

Cymbospondylus a genus of marine reptiles in the order Ichthyosauria. A basal ichthyosaur, *Cymbospondylus* had a very long, eellike tail (about a third of its length). Like other early ichthyosaurs, it had no dorsal fin. The largest species were more than 30 feet long, and it was probably viviparous. Late Triassic, 240–210 Ma.

Cynodesmus a genus of doglike mammals in the extant family Canidae and extinct subfamily Hesperocyoninae. It was long considered the immediate ancestor of *Tomarctus*, but studies since the 1990s indicate a more distant relationship. United States, late Oligocene to early Miocene.

Cynodictis a genus of carnivorous mammals in the family Amphicyonidae, possibly ancestral to many modern carnivores; Europe and Asia, late Eocene to early Oligocene.

Cynodontia "dog tooth," a large group of therapsids in the suborder Theriodontia. They appeared in Africa in the late Permian and were prominent in the line leading to mammals. Among the few synapsids that survived the end-Permian extinction, the cynodonts diversified widely in the Middle Triassic and may have given rise to the chiniquodontids. They were then displaced by mammals before the end of the Jurassic. See also ***Charassognathus*** and ***Procynosuchus***. Global distribution, late Permian to Late Jurassic.

Cynognathus a genus of large early Mesozoic cynodonts in the family Cynognathidae; synonyms: *Lycognathus* and *Lycochampsa*. About 4 feet long, it was a significant predator, with a large and wide-jawed head and a wolflike dentition with strong canines and carnassials. Africa, Antarctica, and South America, Early Triassic.

Cyonasua a genus of small carnivorous mammals in the family Procyonidae. Estimated at 30–50 pounds, it was larger than most procyonids. C*yonasua* was one of the first North American placental carnivores to reach South America. Argentina and Venezuela, late Miocene to Pleistocene, 7–1 Ma.

Cyonosaurus a genus of gorgonopsian therapsids of the late Permian. About 3 feet long, with long canine teeth, it is well-known from two dozen specimens dated between 254 and 252 Ma; there is also recent but inconclusive evidence that it may have survived the end-Permian extinction. South Africa, late Permian.

Cypridea a genus of freshwater podocopid ostracods, possibly related to the modern Cyprididae. *Cypridea* is generally oval, often pitted and tubercular, and some species (*e.g., C. vitimensis*) are sexually dimorphic. Holarctic distribution, Middle Jurassic to Cretaceous.

Cyrtina a genus of small spiriferinid brachiopods in the family Cyrtinidae. Nut-shaped and strongly ribbed, it is notable for a flat triangular area between the hinge line and the beak of the pedicle valve, which is arched with a prominent fold. Cosmopolitan, Silurian to Early Carboniferous.

Cyrtocrinida a disparate extant order of articulate crinoids, generally squat and compact. The order, which flourished in the Mesozoic and has only a few surviving genera, includes unusual forms such as *Hemicrinus* and the extant *Holopus*. North America and Europe, Devonian to Recent.

Cystiphyllum a genus of horn corals, solitary rugose corals in the family Cystiphyllidae. Up to 2 inches long, it had an interior surface consisting of irregular vesicular dissepiments, with the septa reduced to spinose ridges. Global distribution, early Silurian to Late Devonian, 436–376 Ma.

Cystoidea a class of early Paleozoic crinozoan echinoderms, formerly considered blastozoans. The two main orders are the Rhombifera and the Diploporita. They were attached to hard substrates by a stalk and generally had irregular pentameral symmetry, with thecae of many plates and triangular pore openings. They may have given rise to the crinoids (see also **Edrioasteroidea**). Global distribution, late Cambrian to Devonian, with maximum diversity in the Late Ordovician.

Cystoporata "saclike passages," an order of marine bryozoans in the extant class Stenolaemata. They had elongated zooecia on supporting blister-like vesicular structures called cystopores. Global distribution, Ordovician to Permian.

Cythereis an extant genus of podocopid marine ostracods in the family Cytheridae. It has an oval to irregular outline and is generally heavily ridged. Global distribution, Permian to Recent, widespread in the Cretaceous.

Cytherelloidea an extant genus of platycopid marine ostracods in the superfamily Cytherelloidea. Suboval, it has a pitted surface with prominent horizontal lobes. Global distribution, Triassic to Recent.

Cytheropteron a genus of podocopid marine ostracods in the family Cytheruridae. It has an oval to suboval and sometimes irregular shape, generally with a smooth surface. Global distribution, Triassic to Recent.

Cytheruridae a large family of podocopid marine ostracods in the superfamily Cytheroidea; global distribution, Triassic to Recent.

D

Dacrydium an extant genus of conifer trees in the family Podocarpaceae. Australia and New Zealand, Eocene to Recent.

Dactylioceras a genus of ammonoids in the order Ammonitida. Its strongly ribbed shell is relatively narrow and 3 inches high at the most, and it was numerous. It was part of the radiation of ammonitids that followed the extinction of most ceratitid ammonoids at the end of the Triassic. Occurring in the Pliensbachian, always in a stratum just above that of *Amaltheus*, it is a significant index fossil. Global distribution, Early Jurassic, 200–172 Ma.

Daedalosaurus see **Weigeltisauridae**.

Daeodon a genus of artiodactyl mammals in the family Entelodontidae. Mainly a scavenger, it was bison-sized and resembled a giant warthog. The type genus, *D. shoshonensis*, was the largest entelodont; 12 feet long and 6 feet high at the shoulder, it had a skull 3 feet long. United States, Oligocene to middle Miocene.

Dakosaurus "biting lizard," a genus of large marine crocodylomorphs in the clade Thalattosuchia and family Metriorhynchidae. It was up to 16 feet long and a good swimmer, with a finned tail and paddle-shaped limbs. The skull was up to 3 feet long, with a jaw containing dozens of sharp, serrated teeth. *Dakosaurus* was mainly marine, but whether it gave birth at sea or on land is unclear. North and South America, Europe, and Russia; Late Jurassic to Early Cretaceous, 160–135 Ma.

Dalmanellidina the second of the two suborders of brachiopods in the Rhynchonellata order Orthida. Generally punctate, the group appeared early in the Ordovician and diversified widely into the Devonian; some genera survived to the late Permian. Global distribution, Early Ordovician to late Permian.

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Dalmanites a genus of phacopid trilobites in the suborder Phacopina and family Dalmanitidae. From 3 to 6 inches long, *Dalmanites* had large, raised schizochroal compound eyes and a strong tail spine. Its pear-shaped glabella is vaulted and expands slightly forward. Global distribution, Silurian to Early Devonian.

Daonella a genus of marine halobiid bivalves in the order Ostreoida. Placed either in the Halobiidae or the Posidoniidae; the oyster-like *Daonella* is found worldwide in Triassic strata, where several species are index fossils.

Dapedium a genus of actinopterygian fish in the order Semionotiformes and family Dapediidae. A durophagous fish, *Dapedium* had peg-like teeth useful for crushing hard-shelled invertebrates. It was up to 16 inches long, deep-bodied, and protected by thick dermal head bones and a covering of rhombic ganoid scales. North America and Europe, Late Triassic to Late Cretaceous.

Daphoenodon a genus of large carnivorous canids in the family Amphicyonidae; widespread in the United States, late Oligocene to Miocene.

Darwinius masillae a contentious species of early cat-sized primates from about 48 Ma, about 2 feet long. A nearly complete skeleton was found in 1983 in the Messel Shale Pit that has opposable thumbs and fingernails rather than claws; absent are the toothcomb and grooming claws characteristic of more primitive animals. Its authenticity and importance, however, are in dispute, partly because of collection difficulties. Like most specimens from Messel, the specimen of *Darwinius* is part and counterpart of a split bedding plane, covered with resin to preserve it, so that the bones cannot be individually handled and carefully examined. Germany, middle Eocene.

Darwinopterus a genus of pterosaurs in the family Wukongopteridae. Dated at 161 Ma, it is notable for possessing characteristics of both large groupings of pterosaurs, the "rhamphorhynchoids," and their descendants, the pterodactyloids. China, Late Jurassic.

Daspletosaurus torosus "horrible muscular lizard," a North American species of large tyrannosaurid dinosaurs in the subfamily Tyrannosaurinae. Closely related to the later *T. rex*, *Daspletosaurus* grew up to 30 feet long. There is some evidence that it lived in social groups. Alberta and Montana, Late Cretaceous, 77–74 Ma.

Dastilbe a genus of gonorhynchiform fish in the family Chanidae. From 1 to 2 inches long, it has been found in large numbers in the Crato Formation of Brazil. South America and Africa, Early Cretaceous, 125–110 Ma.

Dasyatidae a family of rays in the order Myliobatiformes. Commonly called whiptail stingrays, they are characterized by flattened fin discs and a generally oval outline and also by a venomous stinger at the base of the tail. They may have

originated in the Late Jurassic and were widespread from the early Eocene to the late Miocene. Global distribution, Early Cretaceous to Recent.

Dasyuridae a large family of marsupial mammals in the clade Dasyuromorphia. The dasyurids include *Dasyurus* (quoll), *Sarcophilus* (Tasmanian devil), and other small genera like *Sminthopsis* (dunnart). Australia, Oligocene to Recent.

Dasyuromorphia "shaggy tail," the extant order of mostly carnivorous marsupials that include the Dasyuridae and the extinct Thylacinidae; Australia and New Guinea, early Oligocene to Recent.

Daubentonia the aye-aye, an extant genus of lemur-like strepsirrhine primates, is known only on Madagascar. Although its phylogeny is uncertain, it is generally considered a basal lemuroid. Smaller than the lemurs and similar to the Lorisoidea of Africa and Asia, the nocturnal *Daubentonia* has large eyes and two adaptations for extracting insects from tree bark: forward-slanting incisors and an elongated middle finger. It is generally thought to be descended from the original lemuroid immigrants to Madagascar between the middle Eocene and early Miocene. Some researchers, however, point to similarities between *Daubentonia* and two African primates, *Plesiopithecus* and *Propotto*, suggesting that lorisoid ancestors of the aye-ayes reached Madagascar independently and later than the basal lemuroids.

Davidsonina septosa a spire-bearing species of articulate brachiopods in the class Rhynchonellata, order Spiriferinida, and family Davidsoninidae, significant as an index fossil; Europe, Early Carboniferous.

Daxatina canadensis a species of ceratitid ammonoids in the family Trachyceratidae. Its first appearance marks the beginning of the Late Triassic at 237 Ma. Italy.

Dayiidae a family of brachiopods in the class Rhynchonellata, order Atrypida, and superfamily Dayioidea; Europe, Asia, and North Africa; early Silurian to Early Devonian.

Deccan Traps an area of large volcanic flows in India, mainly basalt, resulting from an eruption near the end of the Cretaceous. It is one of the largest geological features of Earth, covering an area about 200,000 square miles.

Decennatherium a genus of artiodactyl mammals in the family Giraffidae, similar to the later ***Sivatherium***, *q.v*. *Decennatherium* has been known for several decades from several specimens found in Spain and is now well-known from an almost complete skeleton described in 2017. The recent specimen, named *D. rex*, was about 10 feet tall and 7 feet at the shoulder; it has two small ossicones behind its eyes and two longer ones at the back of its skull. Europe, late Miocene, 9 Ma.

Declinognathodus nodiliferus a species of conodonts whose first appearance marks the beginning of the Late Carboniferous (Pennsylvanian) at 323.2 Ma; United States.

Deinocheirus a monospecific genus of primitive theropod dinosaurs in the family Deinocheiridae. At 36 feet long, *D. mirificus* was the largest ornithomimid, with robust forelimbs 8 feet long and hands tipped with three 10 inch claws. It is notable also for its humped back, formed by a sharply arching spine, with a small sail above the hips. Its long, slender snout and stomach contents (including plants and fish scales) indicate that it was omnivorous. Mongolia, Late Cretaceous, 71–69 Ma.

Deinocroton draculi a species of ticks in a proposed new family Deinocrotonidae. Known only from one amber specimen a third of an inch long, *D. draculi* is speculated to have parasitized dinosaurs. Burma, Late Cretaceous.

Deinogalerix "terrible shrew," a genus of omnivorous hedgehogs in the extant family Erinaceidae. Some species grew to the size of a wolf, an example of island gigantism. *Deinogalerix* had a long, thin skull and hair, not the spines of modern hedgehogs. Restricted to the Gargano Peninsula of Italy, which was the location of several islands during the Miocene; Miocene to Pliocene.

Deinonychus antirrhopus a species of theropod dinosaurs in the family Dromaeosauridae. About 11 feet long, with three claws on each manus and pes, it was an efficient predator. Like other dromaeosaurs, it had a sickle claw on the second toe of each pes. *Deinonychus* laid its eggs in open nests, not buried; the eggs are notable for containing pigments like those found in modern birds' eggs. North and South America, Early Cretaceous, 115–108 Ma.

Deinopoidea an extant superfamily of orb-weaving spiders in the order Araneae. They produce a web of cribellate silk that appears to be combed; the web catches insect legs in the same way that the Velcro is fastening fabric works. Fossil specimens of their webs are sometimes found because of insects trapped in them. The earliest-known complete orb web with prey attached (a fly, a mite, a beetle, and a wasp leg) was found in 2005 in a Lower Cretaceous deposit in Spain. Inconclusive phylogenomic research has challenged the monophyly of the Deinopoidea. See also **Araneoidea.** Global distribution, Middle Jurassic to Recent.

Deinosuchus "terrible crocodile," a genus of gigantic crocodilians that lived for less than 10 million years, from about 81 to 73 Ma. About 30 feet long and weighing up to 5 tons, *Deinosuchus* inhabited the shallow sea in the middle of North America, where its diet included dinosaurs and turtles. A five-foot-long skull found in Texas in 1997 bears teeth 5 to 6 inches long. North America, Late Cretaceous.

Deinotheriidae a small family of late Cenozoic elephant-like proboscideans whose most notable feature was a pair of long, backward-curving tusks on the lower

jaw. The three genera in the family are *Chilgatherium, Prodeinotherium*, and *Deinotherium*. With a shorter trunk than that of the modern elephant, they resembled elephants but were not ancestral to them. Their extinction coincided with the worldwide Quaternary extinctions of many large mammals. Europe, Asia, and Africa; late Oligocene to late Pleistocene.

Deinotherium the latest of the three genera of proboscideans in the family Deinotheriidae. The largest land animal of its time, *Deinotherium*, was 15–16 feet high at the shoulder and weighed up to 10 tons. It was a browser and probably had a short, stout trunk, perhaps midway in size between the trunks of modern tapirs and elephants. It replaced the smaller *Prodeinotherium* in the middle Miocene and ranged throughout Europe, Africa, and Asia until its extinction in the Pleistocene.

Deiphon a genus of phacopid trilobites in the family Cheiruridae, widespread in the Silurian. Notable for a set of numerous strong spines and by the warty surface of the glabella, it is similar to *Eldredgeops rana*. Europe and North America, Late Ordovician to Early Devonian.

Deltadromeus a possible genus of theropod dinosaurs, generally placed in Ceratosauria. Agile and probably a fast runner although it weighed up to 2 tons and grew to 26 feet long, it is known only from skeletal fragments and may be a juvenile *Bahariasaurus*. Kem Kem beds, Morocco and Algeria, Late Cretaceous.

Deltatheridium a genus of basal metatherian mammals in the order Deltatheroida and family Deltatheridiidae. About 6 inches long, scansorial, and carnivorous, it has a combination of marsupial and placental characteristics. Mongolia and possibly North America, Late Cretaceous, 80 Ma.

Deltatheroida an order of basal metatherian mammals, near the beginning of the line of descent leading to the marsupials. They were scansorial omnivores and widespread in the Cretaceous. See also ***Gurbanodelta kara***. Central Asia and North America, Early Cretaceous to late Paleocene.

Delthyridina the smaller of the two suborders of brachiopods in the order Spiriferida, distinguished by strong ribbing and a conspicuous fold; global distribution, Cambrian to Permian.

Deltoblastus a genus of blastoid echinoderms in the order Spiraculata. Characterized by a conical shape with high ridges between the broad, depressed ambulacra, it was from 1 to 3 inches long and attached to the substrate. Similar but not directly related to the better-known *Pentremites*, it was one of the last of the Blastoidea, which disappeared at the end of the Permian. Asia, early Permian.

Demospongiae the largest and most diverse class of the phylum Porifera, the sponges. Ranging from encrusting forms to large genera up to 3 feet in diameter,

they comprise 80 percent of known modern sponges. Their skeletons are composed of siliceous spicules, spongin fibers, or both. See also **Sphaeractinoidea;** Cambrian to Recent.

Dendrerpeton acadianum an obscure species of temnospondyl amphibians. Estimated at about 8 inches long and similar to *Amphibamus*, it was an early tetrapod known only from disarticulated fossils. Nova Scotia, Early Pennsylvanian.

Dendrobranchiata a suborder of decapod malacostracan crustaceans. Up to a foot long, with a robust body and many appendages, especially long antennae, they are often called prawns, leaving the Caridea as the true shrimps. Global distribution, Late Devonian to Recent.

Dendrograptus a genus of irregularly branching graptolites in the order Dendroidea; Europe, Asia, and North America; late Cambrian to Middle Devonian.

Dendroid having a branching habit of growth. Dendroid corals form an irregularly branching pattern, separated from each other. Dendroid graptolites form a bushy colony in which the stipes branch irregularly from each other.

Dendroidea an order of sessile branching graptolites that originated in the Middle or Late Cambrian, the earliest order of the Graptolithina. Probably ancestral to the other major graptolite order, the Graptoloidea, which appeared in the Early Ordovician. Most genera of the Dendroidea were benthic, attached by holdfasts to the substrate and often bushy. The order is exemplified by *Dendrograptus, Callograptus,* and *Dictyonema*. Early Cambrian to Early Carboniferous.

Dendropithecus a poorly known genus of early primates in the superfamily Hominoidea and family Dendropithecidae. Similar in some ways to gibbons, it is now considered a stem catarrhine. East Africa, early to middle Miocene.

Denisovans an extinct species of humans in the genus *Homo*. The Denisovans were a relatively small group of hominins who lived in Southern Siberia between 110,000 and 50,000 years ago. They are related to Neanderthals, who are known to have lived between this area and Western Europe up to 40,000 years ago, and they may also have interbred with other hominins, such as *Homo erectus*. This culture supplies more evidence that many types of slightly differentiated hominins coexisted with *H. erectus* for long periods of time.

Dentalina a genus of elongate, curving foraminiferans in either the Nodosariidae or the Lagenidae; global distribution, Permian to Recent.

Dentalium a large extant genus of tusk shells, scaphopod mollusks in the order Dentaliida. *Dentalium* contains about 100 species, 50 of them extinct. Up to 4

inches long, the shell resembles an elephant's tusk, tapered and curving planispirally, with both ends open. Global distribution, Ordovician to Recent.

Denticle (1) serrations on the teeth of other animals, (2) pointed, placoid scales of cartilaginous fish.

Dentition Since teeth fossilize easily and are the most common fossil specimens of many animals, patterns of dentition are very important. The type of tooth often tells a great deal about diet and lifestyle, and the number and types of teeth are often used in classifying animals.

The manner of replacement of teeth is also sometimes a significant descriptive characteristic. Monophyodonty refers to having only one lifetime set of teeth. Diphyodonty refers to having two sets of teeth, one deciduous ("milk teeth") and one permanent, and is one of the characters that differentiate mammals from therapsids. Polyphyodonty is the condition of having an indefinite number of tooth replacements. See also ***Limusaurus***, **brachydont, bradyodont**, **bunodont**, **heterodont**, **hypsodont, lophodont, petalodont**, **sectorial tooth,** and **selenodont**.

Deperetellidae a family of perissodactyl mammals in the superfamily Tapiroidea, ancestral to modern tapirs; Asia, middle to late Eocene.

Derived character a novel character, changed from a preexisting character or condition, which first appears in the most recent common ancestor of a lineage and is passed on to its descendants.

Dermal ossicles bony plates attached to the skin or cuticle of many animals, sometimes constituting an armored covering. Ossicles are found in dinosaurs, reptiles, turtles, echinoderms, and several xenarthran mammals, such as the ground sloth *Paramylodon* and the glyptodonts.

Dermoptera an order of arboreal euarchontan mammals still represented by the extant colugos in the family Cynocephalidae. See also **Galeopithecidae** and **Mixodectidae**. Cosmopolitan, Late Cretaceous to Recent.

Desmatochelys a genus of cryptodiran marine turtles in the extinct family Protostegidae. The older of its two species, *D. padillai*, is the earliest-known sea turtle, 7 feet long and dated at around 120 Ma. South America, Early Cretaceous.

Desmatosuchus a genus of aetosaurs in the family Stagonolepididae. About 16 feet long, the crocodile-like *Desmatosuchus* bore a series of striking spines on its sides, the farthest forward as long as 18 inches and pointing backward. United States, Late Triassic, 230–210 Ma.

Desmostylia "bundle pillar," an order of quadrupedal aquatic perissodactyl ungulates, the only known extinct order of marine mammals. About 6 feet long and up to

450 pounds, they were very similar to proboscideans and modern manatees, but the similarities may be only a result of convergence. Desmostylians' dentition is characterized by forward-pointing incisors and tusks and by closely packed molars resembling a bundle of pillars. See also ***Behemotops*** and ***Paleoparadoxia***. Japan and North America, late Oligocene to early Miocene.

Deuterostomia a superphylum including the phyla Chordata, Echinodermata, and Hemichordata; the hemichordates include the Graptoloidea and Enteropneusta. The earliest deuterostomes are microscopic organisms of the Early to Middle Cambrian, the earliest accepted being *Saccorhytus*, dated at 540 Ma. See also **Vetulicolia**. Early Cambrian to Recent.

Devonian the fourth period of the Paleozoic Era, from 416 to 359 Ma, divided into Early, Middle, and Late Epochs. Known as the age of fish, the Devonian saw a great radiation of marine and freshwater fish, including the first sharks. The first ammonoids developed from the bactritid nautiloids in the Early Devonian. Evolutionarily, the period is most important for its terrestrial developments. Aquatic fish like *Eusthenopteron* in the Middle Devonian gave rise to tetrapods like *Tiktaalik* and *Ventastega* that began to move ashore toward the end of the period. The first insects appeared at the same time as a rapid radiation of terrestrial plant life. At the beginning of the period, the tallest plant was only about 3 feet high, but as the vascular plants spread, trees and even forests appeared. Trimerophytes diversified from the Early to the Late Devonian, probably giving rise to the progymnosperms and ferns and thus ancestral to most modern plants.

Devonian extinction a series of closely spaced extinction pulses during the final 5 million years of the period (some argue for seven events over the last 25 million years). The principal extinctions occurred at the beginning and end of the Famennian Age, respectively, the Kellwasser and Hangenberg Events. Major groups that disappeared included the placoderms and most agnathans. The coral and stromatolite reef-builders were so severely affected that there was little reef-building until the rise of the scleractinian corals in the Mesozoic. The trilobites were especially affected by the Kellwasser event, and only those of the order Proetida survived into the Carboniferous. Some have pointed to global cooling and widespread anoxia in the oceans as a cause of some of these extinctions, but the evidence is inconclusive.

Diacodexis a genus of small Eocene ungulate mammals in the family Dichobunidae. Almost 3 feet long, *Diacodexis* is the earliest-known artiodactyl mammal, although its feet still had five toes, with elongated third and fourth digits. North America, Europe, and Asia; early to middle Eocene.

Diadectomorpha a group of bulky anthracosaurian amphibians closely related to the early amniotes, although their mode of reproduction is still obscure. Reptile-like and among the largest early tetrapods, some herbivorous genera (such as *Diadectes*)

grew up to 10 feet long. North America, Europe, and Asia; Late Mississippian to late Permian.

Diadematoida an extant order of euechinoid sea urchins. They are characterized by long, slender, hollow spines and ten buccal plates around the mouth, with either flexible or rigid tests. Cosmopolitan but mainly Europe, Late Triassic to Recent.

Diademopsis a genus of primitive echinoids in the order Pedinoida and family Pedinidae, a common echinoid in Europe during the Early Jurassic. Generally 1–2 inches wide, they are characterized by tessellate plating; long, slender spines; and a lantern with broad, grooved teeth. Close to the ancestry of all euechinoids. Cosmopolitan but mainly Europe, Late Triassic to Early Jurassic.

Diagenesis in geology, a term for the process of changes in a rock over time, such as a sedimentary rock becoming metamorphosed. In paleontology, diagenesis refers to the final taphonomic process undergone by a fossil, especially to the process of mineralization, which varies widely according to the burial site (such as in sediment, amber, tar, hydrothermal vent, or volcanic material). Successive diagenetic events may occur if the burial environment is disturbed. See also **taphonomy**.

Diania cactiformis a worm-like animal dated at about 520 Ma, related to an extinct group of armored lobopods. With robust spiny limbs, possibly jointed, it may be a forerunner of true arthropods. Chengjiang, China, early Cambrian, ca. 518 Ma.

Dianulitidae a family of Stenolaemate bryozoans in the extinct order Cystoporata; North America, Europe, and Asia; Ordovician and Silurian.

Diapsida "two arches," the stem group of early amniotes that gave rise to crocodiles, dinosaurs, lizards, snakes, and probably turtles. They are generally identified by two temporal fenestrae behind each eye, except that modern snakes and lizards have lost one or both of these openings. The diapsids appeared late in the Pennsylvanian, after the first synapsids.

Diatoms a kind of glassy-shelled algae in the class Bacillariophyceae. Generally flat and round-like two pie plates stuck together; diatoms constitute an important area of study in micropaleontology. They appeared in the fossil record in the early Jurassic and exist globally in marine and freshwater bodies of water. See also ***Stephanodiscus***.

Diatryma see ***Gastornis***.

Dibunophyllum a genus of generally solitary rugose corals in the family Aulophyllidae. It was large and cono-cylindrical in shape. North America, Europe, Africa, and Asia; Late Devonian to Late Pennsylvanian.

Dicellograptus a widespread and varied genus of graptoloids in the family Dicranograptidae. Part of the leptograptid fauna is an important graptolite index fossil group in the Late Ordovician. Global distribution, Middle to Late Ordovician.

Diceratherium "two-horned beast," a genus of large perissodactyl mammals in the family Rhinocerotidae. It weighed about a ton and is notable for a pair of horns side by side on the nose, the first rhinocerotoid to develop horns. Widespread in North America, Europe, and Asia; Oligocene to Miocene.

Dichobunidae a family of primitive artiodactyl ungulate mammals. They were small, generally 2–3 feet long, and were omnivorous, with bunodont upper teeth; they are typified by ***Diacodexis****, q.v.* North America, Europe, and Asia; early Eocene to late Oligocene.

Dichograptid fauna an important fossil group of the Ordovician, including the many-branched *Dichograptus* and other graptoloid index fossils; see **Graptolithina**.

Dichograptus octobrachiatus an unusual species of graptolites, living in a circular colony 3–4 inches in diameter. Its eight equal-length stipes were slender, with very small individual thecae. North America, Europe, and Australia; Early Ordovician.

Dickinsonia an enigmatic genus of flat-bodied fossils in the family Dickinsoniidae. An iconic member of the Ediacaran biota, it has been variously considered to belong to the fungi, the coelenterates, or an otherwise unknown class; it is now generally considered an animal of uncertain affinities. The body is a bilaterally symmetrical ribbed oval, usually a few inches long, but the largest known was about 3 feet long and 2 feet wide. Although hundreds of specimens have been studied, little is known about its mode of life. Its trace fossils, generally ferruginous impressions on the underside of an overlying stratum, have been dated between 579 and 555 Ma, making it the earliest-known macroscopic animal. Australia and Eastern Europe, Ediacaran.

Dicksonia an extant genus of pteridophyte tree ferns in the order Cyatheales and family Dicksoniaceae; Australia and New Zealand, Jurassic to Recent.

Dicoelosia a genus of small rhynchonellate brachiopods in the order Orthida, formerly called *Bilobites*. Biconvex and strongly bilobed, it grew to only a third of an inch long and was symmetrical in two planes. Important stratigraphically in the Late Ordovician and the Silurian. Global distribution, Late Ordovician to Early Devonian.

Dicraeosauridae a family of relatively small sauropod dinosaurs, closely related to the Diplodocidae. The family includes the genus *Dicraeosaurus* and the species *Brachytrachelopan mesai* and *Amargasaurus cazaui*; another possible dicraeosaurid (the only one from North America) is ***Suuwassea emilieae***, *q.v.* South America and Africa, Middle Jurassic to Early Cretaceous.

Dicranograptus "two-headed," a genus of bilateral graptolites in the order Graptoloidea and family Dicranograptidae. A planktic member of the leptograptid fauna, it typically has stipes that branch only once, with small, convoluted thecae. Cosmopolitan, Early to Late Ordovician.

Dicranurus "two-head-tail," a genus of spiny trilobites in the order Odontopleurida and family Odontopleuridae. *Dicranurus* was a very spinose trilobite, with long pleural and genal spines and two distinctive thick, curling spines behind the head. Its body was an inch long, but several spines were 2 inches long. North America, North Africa, and Australia; middle Silurian to Lower Devonian.

Dicroidium a genus of woody seed ferns in the order Peltaspermales and family Corystospermaceae. Its leaves have been found attached to branches, and some reports refer to it as a tree dozens of feet high, but its fossils are known mainly as leaves of a wide variety of types. Known at least as far back as the late Permian in Jordan, it became widespread in Gondwana throughout the Triassic before declining in the Early Jurassic. The latest specimens, from Antarctica, are dated about 175 Ma. Late Permian to Early Jurassic.

Dictyoclostus a genus of articulate strophomenate brachiopods in the family Productidae. Up to 2 inches across, *Dictyoclostus* is marked by a network of fine lines, grooves, and spines; its pedicle valve is strongly convex and beaked. *D. americanus* is an index fossil in the Late Pennsylvanian. Global distribution, Early Carboniferous to Permian.

Dictyonellida the larger of the two orders of articulate brachiopods in the class Chileata, with a fine network of rays on the surface of the shell; Ordovician to Permian.

Dictyonema "net thread," an important genus of many-branched dendroid graptolites. It was sessile, with a net-like structure and many small thecae. Late Cambrian to Early Ordovician.

Dictyoptera a superorder of insects, including the extant Blattodea (roaches and termites) and Mantodea (mantises) and the extinct Alienoptera.

Dictyospongia a genus of hexactinellid reticulate sponges in the family Dictyospongidae, distinguished by a smooth reticulum and an inverted cone shape; North America, Silurian to Carboniferous.

Dictyothyris a genus of articulate brachiopods in the extant order Terebratulida and superfamily Terebratuloidea. It had an erect beak and large pedicle aperture. Middle Jurassic to Early Cretaceous.

Dicynodontia a clade of herbivorous therapsids. Short and strongly built, with some genera such as *Placerias* growing two tusks, they appeared in the middle of the Permian. Along with the theriodonts, they were the sole synapsid survivors of the end-Permian extinction. The largest and most successful of the nonmammalian therapsids, they then diversified globally in the Early and Middle Triassic. The largest of the dicynodonts was the Late-Triassic *Lisowicia*, estimated at 15 feet long and 9 tons. They were largely replaced by traversodont and cynodonts at the end of the Middle Triassic, and most survivors disappeared in the end-Triassic extinctions, with some possibly surviving in Australia into the Cretaceous.

***Dicynodon* zone** a paleoecological term for a terrestrial faunal assemblage in the time just before the end-Permian extinction. Based mainly on research in the Karoo Basin of South Africa, it had a mature and complex food web dominated by therapsids. The earliest herbivorous therapsids such as *Dicynodon* and the numerous carnivores that preyed on them (such as the therapsid therocephalians and gorgonopsians) flourished in a subtropical environment characterized by the glossopteris flora and a monsoonal climate.

Didelphidae "two wombs," the opossums, an extant family of arboreal marsupials in the order Didelphimorphia. Didelphids probably originated in North America in the Early Cretaceous and were abundant in the Late Cretaceous but became extinct there in the Miocene. After migrating in the Eocene to Europe and spreading worldwide, they again appeared in North America near the beginning of the Pleistocene.

Didelphimorphia an extant order of American marsupials, now represented chiefly by the family Didelphidae. North and South America, Paleocene to Recent.

Didelphodon a genus of marsupialiform mammals in the family Stagodontidae. The type species *D. vorax*, although only as large as a small badger, is estimated to have had a stronger bite than a hyena. North America, Late Cretaceous, 73–66 Ma.

Didolodontidae an extinct family of middle-sized condylarths in the superorder Meridiungulata. About 2 feet long, they were scansorial insectivores. South America, Paleocene to early Miocene.

Didus see ***Raphus cucullatus***.

Didymograptus "double branch," one of the larger graptolites, a graptoloid genus identified by its two very long branches, often referred to as the "tuning fork" graptolite; Early to Middle Ordovician.

Dielasma a widespread genus of articulate brachiopods in the order Terebratulida. Less than an inch long, with a biconvex, rather smooth shell, it was suboval, with the pedicle valve much larger than the brachial valve. Global distribution, Mississippian to Permian.

Digitigrade walking on toes or claws, with the rear part of the foot raised.

Diictodon one of the most successful synapsids of the Permian, a genus of herbivorous dicynodont therapsids in the family Pylaecephalidae. Less than 2 feet long and armed with a pair of tusks extending down from the upper jaw, *Diictodon* burrowed helical tunnels as deep as 5 feet where articulated skeletons have been found. Known mainly from Southern Africa but also Asia, 260–254 Ma.

Dikelocephalus a genus of large Sunwaptan asaphid trilobites in the family Dikelocephalidae. Up to 16 inches long, it had a broad cephalon and a very broad pygidium with spines at its corners. United States, latest Cambrian.

Dikika baby name given to an almost complete fossil skeleton of a female child of nursing age. Dated at 3.3 Ma, it is generally classified as *Australopithecus afarensis*, with some claiming a closer relationship to *Au. africanus*. Also referred to as "Selam," the skeleton includes a complete torso, a face, and some leg bones and was probably bipedal. It was found in 2000 in the Dikika region of Ethiopia, across the Awash River from Hadar, a few miles from where the *Au. afarensis* skeleton called Lucy was found.

Dilong a monospecific genus of small dinosaurs in the family Proceratosauridae. In the Jehol biota, it is generally considered an early tyrannosauroidea. From 5 to 6 feet long and with a feather-like body covering, *D. paradoxus* is known from almost complete specimens from the Lower Cretaceous Yixian Formation. China, 125 Ma.

Dilophosaurus "two ridges," a monospecific genus of theropod dinosaurs known only from the Kayenta Formation of Northern Arizona. Relatively small but an efficient predator, *D. wetherilli* was about 23 feet long and weighed about 1100 pounds, with long teeth. Its most distinctive feature is a pair of crests along the front of its skull. United States, Early Jurassic, 193 Ma.

Dimaitherium a monospecific genus of early paenungulate mammals in the order Hyracoidea. *Dimaitherium patnaiki*, discovered in 2010, is the earliest-known hyracoid. Fayum, Egypt, late Eocene, 37 Ma.

Dimetrodon a genus of large synapsids in the family Sphenacodontidae, well-known for its very large spinal fin, which gives it the nickname "sailbacked." Most species of *Dimetrodon* ranged from 6 to 15 feet long, and it was an apex predator. It is named for its unusual heterodont dentition, having several types of teeth in a large jaw. The sail may have regulated body temperature, but recent researchers have challenged that theory; other theories also have little support. North America and Europe, early Permian, 295–270 Ma.

Dimorphic a term for a species that has two distinct forms, most often for sexual dimorphism, having distinguishing features

between male and female individuals. Although few organisms in the Paleozoic fossil record can be identified as sexually dimorphic, sexual differences can be identified in ostracods back to the Ordovician and of course more easily for organisms closer to the present. Sexual dimorphism has often resulted in male and female forms being interpreted as different species, a mistake usually corrected by examination of a greater number of specimens.

Dimorphodon a genus of rhamphorhynchoid pterosaurs. It had a wingspan of almost 5 feet, a large head, and three large claws on its wings. *Dimorphodon* is named for its heterodont dentition, having sharp, protruding anterior teeth and also shorter and flatter teeth toward the back of the jaw. The type species is *D. macronyx*, and a possible second species (*D. weintraubi*) was named in 1998. Europe and possibly Mexico, Early Jurassic.

Dimylidae an extinct family of insectivorous erinaceomorph mammals. Between 4 and 8 inches long, they are distantly related to the modern desman and hedgehog. Known only from the Miocene in Europe.

Dinaelurus a genus of feliform carnivores in the family Nimravidae, known only from a relatively broad skull and partial skeleton found in the John Day Fossil Beds; United States, Oligocene to early Miocene.

Dinichthys terrelli see ***Dunkleosteus***.

Dinocephalia "terrible head," a clade of large therapsids of the Permian. Ranging from dog-sized (*Pampaphoneus biccai*) to more than 15 feet long (*Moschops*), they were the least advanced therapsids, very similar to their ancestors, the pelycosaurs. Among the largest animals of the Permian, some were herbivorous and others carnivorous. The dinocephalians are known only from the period 272 to 260 Ma, becoming extinct with no known descendants. See also ***Titanophoneus potens***. South America, Europe, Asia, and South Africa; middle to late Permian.

Dinocerata an order of large, herbivorous ungulate mammals, generally considered to have one family, the Uintatheriidae. The large-browser niche of the Dinocerata was gradually taken over in the late Eocene by the brontotheres. Laurasia, late Paleocene to late Eocene.

Dinochelys whitei a species of Mesozoic cryptodiran turtles tentatively assigned to the family Pleurosternidae. It is known from a well-preserved foot and several adult and juvenile carapaces; total adult length is estimated to have been 2 feet. United States, Morrison Formation, Late Jurassic.

Dinoflagellates "whirling whips," an enigmatic group of protists. Second only to diatoms as primary producers in the oceans, dinoflagellates are also present in brackish and freshwater environments. On the basis of biomarkers, they are thought

to have appeared in the Late Proterozoic or early Cambrian, but many suggested specimens from the middle Paleozoic have been rejected (see ***Arpylorus***). Known more fully from the Triassic to Recent.

Dinornithidae a family of moas, giant flightless ratite birds in the extant infraclass Palaeognathae and extinct order Dinornithiformes. The largest of the moas grew to about 12 feet high and weighed more than 500 pounds; alone among the ratites, they lacked wings entirely. Moas displayed a wide degree of sexual dimorphism, the female being much larger than the male. Along with the other family of moas, the Emeidae, they were extant in New Zealand from the Pleistocene until a few centuries ago, when the last of the moas were killed off by the Maori inhabitants. New Zealand, Miocene to Recent.

Dinorthis a genus of Rhynchonellata brachiopods in the order Orthida and family Plaesiomyidae. Up to 1 inch long, it was biconvex, slightly strophic, and finely ribbed. Global distribution, Middle to Late Ordovician.

Dinosaur cove a location on the coast of Victoria in Southeastern Australia that has produced specimens of several dinosaurs, including *Leaellynasaura*. The site was within the Antarctic Circle during the Cretaceous.

Dinosauria a large and diverse group of ornithodiran archosaurs that dominated terrestrial life in many parts of the world for almost 160 million years, from the Late Triassic to the end of the Mesozoic. Dinosauria has traditionally been taken as including two orders, the "lizard-hipped" Saurischia and the "bird-hipped" Ornithischia. They evolved from basal archosaurs in the Late Triassic, probably between 235 and 220 Ma, and became widespread in the Jurassic. See **Dinosauromorpha.**

The Theropoda, mostly carnivorous and among the earliest dinosaurs, are generally classified as belonging to the Saurischia. In 2017, however, a large-scale reorganization proposal of the Dinosauria argued that the theropods are a separate group that shares more traits with the Ornithischia; this proposal would place them with the Ornithischia in the revived clade Ornithoscelida**.** Other research between 2009 and 2018 sees the three groups in varying relationships to each other. The theropods, which include the coelurosaurs, are considered the most likely ancestors of birds.

Ranging from rat-sized to whale-sized, various families of dinosaurs radiated in the Jurassic into almost all the terrestrial ecological niches, and those of the clade Titanosauria include the largest terrestrial animals known. The areas most prolific of dinosaur fossils are around the Western Interior Seaway of North America; several sites in North Africa and Southern Africa; the Chinese provinces of Mongolia, Yunnan, Henan, Liaoning, and Sichuan; and several provinces in Patagonian Argentina.

No dinosaurs became completely marine animals, but most were probably capable of swimming, as swim tracks in Spain and Utah have shown. It seems probable

that all dinosaurs were oviparous, often burying the eggs. Some genera have left clear evidence of nest-building, and some seem to have cared for the hatchlings. (See **Auca Mahuevo**, **Egg Mountain,** ***Maiasaura*****,** ***Oviraptor***, **Titanosauria**, and ***Troodon***.) The number of dinosaur species declined toward the end of the Cretaceous, and none survived the end-Cretaceous extinction.

Dinosauriformes a clade of archosaurian reptiles that includes the clade Dinosauria (including birds), *Marasuchus*, and the Silesauridae.

Dinosauromorpha a clade of archosaurian reptiles that includes the Dinosauriformes and the Lagerpetidae. They flourished in the Middle Triassic and coexisted with the basal dinosaurs up to the end of the Triassic. Several basal dinosauromorph archosaurs have been identified as forerunners in the Middle and Late Triassic of the basal dinosaurs in the clade Dinosauriformes (see, e.g., ***Ixalerpeton, Lagosuchus*****,** and ***Lewisuchus***). For further details on Dinosauromorpha, see ***Asilisaurus, Buriolestes, Lagerpetidae, Marasuchus***, ***Saltopus,*** **Silesauridae,** and ***Teleocrater***.

Dinosaur National Monument a large Konzentrat-Lagerstätte on the border of Colorado and Utah that contains several hundred important fossil sites from near to the end of the Jurassic. The fossils occur mainly in strata of the Morrison Formation and consist mainly of dinosaurs and other large vertebrates. The museum is especially known for a wall 200 feet long that displays hundreds of partially relieved dinosaur bones in a Morrison bonebed dated between 155 and 147 Ma. United States, Late Jurassic.

Dinosaur Park Formation the youngest member of the Belly River Group of Southern Alberta. In Dinosaur Provincial Park, it overlies the Oldman Formation and is overlain by the Bearpaw Formation. Canada, Late Cretaceous, 77–76 Ma.

Dinosaur Provincial Park a World Heritage Site in Southern Alberta. Renowned for its fossil assemblage from the Campanian Age of the Cretaceous, it is the richest source of Late Cretaceous dinosaurs in the world. Its geological formations, two terrestrial (Oldman and Dinosaur Park) and one marine (Bearpaw), were laid down between 77 and 75 Ma. They contain a great diversity of fossils besides dinosaurs, yielding a good picture of the ecosystems of the middle to late Campanian.

Diogenornis a basal genus of rheas in the family Rheidae. The earliest-known ratite, it was about two-thirds the size of the modern rhea. Similar to the modern tinamou, it had a narrow beak and larger wings than most ratites. Brazil, late Paleocene to early Eocene.

Diomedeidae the albatrosses, a family of large seabirds in the order Procellariiformes. The largest extant seabirds, several species of albatrosses are

known as far back as the Eocene in the Austral realm and as far north as Hawaii and Washington in the United States. Early Eocene to Recent.

Diphyodonty see **dentition**.

Diplacanthida one of the two suborders of acanthodian fish in the order Climatiiformes.

Diplacanthus a genus of small, edentulous acanthodian fish in the family Diplacanthidae. It is named for two prominent and deeply embedded dorsal spines, paired with smaller ventral spines. North America and Europe, restricted to Early Devonian.

Diplichnites the generic name for a type of trace fossil

consisting of two parallel rows of tracks. It differs from ***Protichnites*** only in the absence of a medial furrow and could be made by the same animal.

Diplobathrida an order of crinoids in the subclass Camerata, distinguished by a conical or dicyclic cup and two circlets of plates; global distribution, Middle Ordovician to Late Mississippian.

Diploblastic a term referring to animals whose blastula is composed of two germ layers, the ectoderm and endoderm. The principal diploblastic animals are the Cnidaria and Ctenophora.

Diplocaulus a genus of large, flattened, and net-like amphibians in the extinct subclass Lepospondyli and order Nectridea. About 3 feet long, it had the nectridean boomerang-shaped skull. *Diplocaulus* is well-known from petroleum-bearing formations in the United States. Late Carboniferous to late Permian.

Diplodocidae a family of generally large sauropod dinosaurs, closely related to the smaller Dicraeosauridae. With a very long neck and a long tail, the diplodocids include a great variety of sizes, including some of the largest dinosaurs. Representative genera: *Apatosaurus, Barosaurus, Diplodocus,* and *Supersaurus.* North and South America, Africa, and Europe; Middle Jurassic to Early Cretaceous.

Diplodocus "double-beam," a genus of very large sauropod dinosaurs in the family Diplodocidae. The name refers to the two rows of ski-like bones on the underside of the tail vertebrae, which helped to support an extremely long tail. One of the largest dinosaurs, *Diplodocus*, reached lengths of more than 90 feet; its head, however, was only 2 feet long and is notable for its tiny teeth in a long jaw. The largest species, *D. hallorum*, was formerly called *Seismosaurus*. North America, Late Jurassic.

Diplograptid fauna one of the important graptolite faunas of the middle Paleozoic, characterized especially by the diplograptid pattern of long, feather-like stipes. See **Graptolithina**. Global distribution, Middle Ordovician to early Silurian**.**

Diplograptus a genus of scandent biserial graptolites in the order Graptoloidea. It is notable for a cap-shaped float to which feather-like stipes containing large assemblages of zooids were attached. Cosmopolitan, Ordovician, and Silurian.

Diploid double or twofold, especially having two sets of genes and two of chromosomes; see **haploid**.

Diplomystus "double whiskers," a genus of primitive herring-like fish in the order Clupeiformes. Generally small but some species 2 feet long, it is distantly related to modern herrings and sardines. It is well-known from the Green River Formation in Wyoming, in association with *Knightia*. Global distribution, Early Cretaceous to early Eocene.

Diplopoda an extant class of myriapod insects that includes the millipedes. Generally detritivorous, they have chewing mouth parts, and they are named "double foot" because they typically have two pairs of legs on each body segment. See also **Archipolypoda** and ***Arthropleura***. Global distribution, Silurian to Recent.

Diploporita a middle Paleozoic class or subclass of blastozoan echinoderms, probably descended from the Eocrinoidea. The Diploporita are similar to the Rhombifera and are distinguished especially by paired pores in the thecal plates. Global distribution, Early Ordovician to Middle Devonian.

Diplotrypa "double hole," a genus of stenolaemate bryozoans in the order Trepostomata. It generally forms a massive, dome-shaped colony up to 4 inches across, composed of circular tubes inhabited by autozooids. *Diplotrypa* is named for these holes and the larger holes bored in the surface by other organisms. Global distribution, Early Ordovician to middle Silurian.

Diplura "twintail," an extant order of eyeless hexapods in the class Entognatha; also commonly called telsontails. Superficially similar to springtails (Collembola), Diplurans have two pairs of appendages, two antennae and two cerci, in most genera all equally long. The order is divided into three families: Campodeidae, Japygidae, Parajapygidae, and Testajapygidae. Global distribution, Carboniferous to Recent.

Dipneusti see **Dipnoi.**

Dipnoi a long-lived order of bony fish, one of the oldest extant groups of animals. The Dipnoi flourished from the Early Devonian to the Triassic, declining since then but still represented by the tropical freshwater lungfish.

Dipodidae the jerboas, an extant family of primitive omnivorous rodents in the infraorder Myomorpha. From 2 to 10 inches long, some with tails three times longer than their body, they are notable for their bipedal jumping ability. North America, Europe, Asia, and Africa; Eocene to Recent.

Diprotodon a genus of marsupial mammals in the family Diprotodontidae. The largest marsupial known, *Diprotodon* was 10–12 feet long, weighed 3 tons, and was more than 6 feet high at the shoulder. Its clawed forefeet turned inward like those of its descendant the wombat, and it browsed on leaves and grasses. It inhabited open and wooded grasslands across the entire continent of Australia from the early Pleistocene to about 45,000 years ago. The date of its extinction is disputed, however, with some reports that it may have still been present as late as 28,000 years ago.

Diprotodontia an extant, very diverse order of herbivorous marsupial mammals, generally considered restricted to Meganesia. The order includes kangaroos and wallabies (see **Macropodidae**), koalas (see **Phascolarctidae**), wombats (see **Vombatidae**), and others. The largest were the extinct Diprotodontidae (see ***Diprotodon***). Australia, Tasmania, and New Guinea; Oligocene to Recent.

Diprotodontidae a family of herbivorous Australian marsupials in the extant order Diprotodontia. The family includes genera that are similar to placental hippopotamuses and rhinoceroses. The last of the Diprotodontidae became extinct about 11,000 years ago. Australia, late Oligocene to Pleistocene.

Diptera "two wings," a large order of insects considered the true flies, estimated to contain more than a million species, about 125,000 of them named. Dipterans are distinguished from other flying insects by having only one pair of wings, which are attached to the first thoracic segment; the second pair evolved into balancing organs. None have stings, but they generally have sucking mouth parts and can bite. They seem to have evolved much later than the earliest insects, appearing only in the Triassic. Early dipterans are numerous in the insect fauna of the Madygen Formation of Kyrgyzstan. Global distribution, Middle Triassic to Recent.

Dipteronotus a genus of ray-finned fish in the family Perleididae. From 2 to 4 inches long, the freshwater and marginally marine *Dipteronotus* was abundant in the Grès à Voltzia and is also known from a few other occurrences in Europe. Middle to Late Triassic.

Dipterus a genus of bony sarcopterygian fish in the order Dipnoi. About 14 inches long and having a lung, it also closely resembles the modern lungfish in other respects. It is known only from strata of the uppermost Devonian; Europe and Australia, Late Devonian.

Disasteridae a family of irregular euechinoids in the superorder Atelostomata. A stem group of atelostomates, they are generally ovoid, sometimes heart-shaped. Europe, Jurassic and Cretaceous.

Disaster taxon a group of organisms that survive a mass extinction and flourish in the ensuing period of hundreds of thousands of years after the extinction. See, for example, ***Claraia***, ***Lystrosaurus***, and **Trigonodidae**.

Discinoidea a long-lived superfamily of inarticulate brachiopods in the order Lingulida. Distinguished by a cap-shaped, discoidal brachial valve, they were especially widespread from the Ordovician to the Devonian. Global distribution, late Cambrian to Recent.

Discoidiidae a family of globular or conical euechinoids in the extinct order Holectypoida; Jurassic to Cretaceous.

Discosauriscus a genus of aquatic stegocephalian seymouriamorph stem-tetrapods in the family Discosauriscidae. Estimated at 10–16 inches long, flattened, with wide jaws, and similar to its larger cousin *Seymouria*, it is named for a small discoidal structure in the vertebrae. *Discosauriscus* is known definitively only from several hundred juvenile specimens found in the lacustrine deposits of the Boskovice Furrow site in the Czech Republic, where the genus constituted a near monoculture. Early Permian, 299–290 Ma.

Discoserra a genus of actinopterygian fish in the small order Guildayichthyiformes, proposed as a possible stem neopterygian. Its circular body is more than 12 inches in diameter and is characterized by rhombic ganoid scales and small forward-facing hooks on the dorsal scute. United States, Early Carboniferous.

Disjunct endemism the ecological occurrence of a species in a unique geographic range and nowhere else in the world.

Disparida a contentious group of early crinoids, traditionally considered an order in the discarded subclass Inadunata; its placement is now disputed. North America and Europe, Early Ordovician to Permian.

Dissorophoidea a superfamily of temnospondyl amphibians considered possibly ancestral to the Lissamphibia. Several highly distinct groups comprise the Dissorophoidea: the Olsoniformes, Amphibamidae, Branchiosauridae, and Micromelerpetidae.

Distacodontidae a family of primitive conodonts identified mainly by a fang-like structure resulting from separation of the lamellae of the teeth, formerly called Distacodidae. Global distribution, Ordovician to Silurian.

Distal see **proximal**.

Ditomopyge a genus of small proetid trilobites in the family Phillipsiidae, one of the last of the trilobites. Only an inch long, it had strong genal spines, a broad and distinctively furrowed glabella, and a fused pygidium. Global distribution, Late Carboniferous to the end of the Permian.

Division a level of classification used in botanical taxonomy, the equivalent of an animalian phylum.

Dizygopleura a genus of platycopid marine ostracods in the family Kloedenellidae. Its oval to suboval shell had a vertically lobed and generally pitted surface. North America and Russia, Silurian to Early Devonian.

Djarthia murgonensis a species of australidelphian marsupial mammals, known only from fragmentary remains but considered the earliest-known marsupial. Tingamarra fauna, Queensland, Australia; early Eocene.

Docodonta the shortest-lived and least diverse order of mammals in the Mesozoic. Slightly larger than mice, in the Middle and Late Jurassic, they radiated mainly in Laurasia but almost globally. Their rectangular, multi-cusped teeth were well-adapted for crushing and grinding; some genera may have been aquatic. Middle Jurassic to Early Cretaceous.

Docofossor brachydactylus a species of early mammaliaformes in the order Docodonta. Found in the Tiaojishan Formation and dated at about 160 Ma, the 6-inch-long *Docofossor* is the earliest-known burrowing mammaliaform. The species name refers to it having a reduced number of phalanges and short but wide fingers adapted to digging. Yanliao biota, China, Late Jurassic.

Docoglossa see **Patellogastropoda**.

Dodo see **Raphus**.

Doedicurus "pestle tail**,** a genus of xenarthran mammals in the subfamily Glyptodontinae. The largest glyptodont at 13 feet long and 5 feet high, *Doedicurus* had a long tail with a spiked tail club. It is known only from Southern South America, becoming extinct about 11,000 years ago. Late Pleistocene to Holocene.

Dokophyllum a genus of solitary rugose corals in the family Ketophyllidae. A rhizosessile horn coral, *Dokophyllum* produced root-like holdfasts that anchored it to the sediment. It was cono-cylindrical and sometimes trochoid in shape. North America, Europe, and Asia; middle to late Silurian.

Dolatocrinus springeri a species of cameratan crinoids in the family Melocrinidae. United States and Australia, Early to Middle Devonian.

Dolichopodidae a large family of long-legged flies, brachyceran dipterans in the superfamily Empidoidea. The family includes about 7000 described species, most with long legs, generally small with prominent eyes and a metallic coloration. Global distribution, Cretaceous to Recent.

Dollocaris ingens an enigmatic species of small arthropods, tentatively placed in the proposed group Thylacocephala. It was probably 5–8 inches long and is especially notable for its very large and complex eyes, each of which was about one-fourth of the body length. La Voulte-sur-Rhône, France, Middle Jurassic.

Doliodus problematicus a species of bottom-dwelling shark in the family Omalodontidae. A specimen found in New Brunswick and dated at 409 Ma is the oldest intact shark fossil, earlier sharks being known mainly from their teeth. It is similar to the modern angel shark but is notable for a pair of inch-long bony spines on the front edge of the fins behind the head, reminiscent of the acanthodian fish of the Silurian. Canada, Early Devonian.

Domeykosaurus chilensis see ***Atacamatitan***.

Dorsal situated on or near the upper surface of an animal.

Dorudon a genus of archaeocete whales in the family Basilosauridae. Like other basilosaurids, it was notable for a blowhole halfway to its eyes, an evolutionary step toward the crown cetacean blowhole on the top of the head. Smaller and more dolphin-like than *Basilosaurus*, it was completely aquatic and had a rudimentary tail that was almost a caudal fluke. Egypt, late Eocene.

Dorygnathus a genus of small basal pterosaurs in the family Rhamphorhynchidae. It had heterodont teeth of several types and a wingspan of about 4 feet. It is known only from several sites in France and Germany, especially several complete skeletons from the Holzmaden site. Europe, Early Jurassic.

Dorypterus "spear fin," a genus of advanced palaeoniscid fish in the family Dorypteridae. It was 8 inches long, with a high dorsal fin almost as long as its body. Europe, late Permian.

Doushantuo Formation an important Ediacaran Konservat-Lagerstatten in Guizhou Province, Southern China. Dated in the period 600–550 Ma, the formation is notable for its exceptional preservation of Ediacaran phosphatic fossils and earlier Cryogenian acritarch fossils.

Douvilleiceras a genus of ammonoids in the order Ammonitida and family Douvilleiceratidae. Between 3 and 4.5 inches in diameter and an inch wide at the aperture, it was evolute and very strongly ribbed, with sharp tubercles and even spines. Its species were widespread from Early to Late Cretaceous, the type species *D. mammilatum* (109–105 Ma) being the most common. Global distribution, Cretaceous, 125–89 Ma.

Dracopelta an early genus of ankylosaurian dinosaurs. Known only from partial skeletal remains with scutes, *Dracopelta* may have been 6 feet long. It had the typical barrel-shaped body of ankylosaurians as well as armor plates of several types, some 5–6 inches wide, but it cannot yet be assigned to either the Ankylosauridae or the Nodosauridae. Portugal, Late Jurassic or Early Cretaceous, 150–140 Ma.

Dracorex a proposed genus of ornithischian dinosaurs in the family Pachycephalosauridae. It is known from only one specimen, a skull and several vertebrae. Its flat, heavy skull and snout are covered with small (possible immature) spikes, and some have argued that the specimen is simply an immature *Pachycephalosaurus*. South Dakota, Late Cretaceous, 71–66 Ma.

Dreadnoughtus schrani a species of titanosaurian sauropod dinosaurs known from two partially articulated specimens found in Patagonia in 2005 and described in 2014. About 70 percent of its skeleton is known from the two specimens, making it the most completely known of the largest dinosaurs. Up to 85 feet long and 30 feet tall, it has been suggested as the largest land animal known, but its weight is disputed, variously estimated at between 40 and 60 tons. Argentina, Late Cretaceous, 84–66 Ma.

Drepanaspis "sickle-shield," a genus of heterostracan fish in the family Psammosteidae. With wide-spaced eyes and a row of spines all along its spine from neck to tail, it was named for the sickle-shaped anterior outline of its flattened, semicircular head. It is well-known from the Hunsrück Slate of Germany, Early Devonian, 410 Ma.

Drepanella a stratigraphically important genus of ostracods in the family Drepanellidae. One of several index fossils in the genus is *Drepanella crassinoda* of the Ordovician. North America and Europe, Ordovician to Devonian.

Drepanellidae a family of possibly paleocopan ostracods in the suborder Beyrichicopina. North America and Europe, Ordovician to late Permian.

Drepanosauridae a family of unusual reptiles in the order Protorosauria. Up to 2 feet long, drepanosaurs are characterized by a sickle-shaped structure at the tip of a prehensile tail, elongated limbs adapted to climbing, and a dorsal neural hump. Although generally found in moist environments, specimens were discovered in

2013 in a site in Utah that in the Triassic was a desert oasis. North America, Late Triassic, 225–215 Ma.

Drinker nisti a genus of small ornithischian dinosaurs in the clade Neornithischia. It is poorly known because of lack of detailed description since it was named in 1990, but it seems very similar to *Othnielosaurus*. About 6.5 feet long, with small forelimbs, it was bipedal and herbivorous. Wyoming, United States; Late Jurassic, 151–146 Ma.

Dromaeosauridae "running lizard," a family of feathered, carnivorous ornithischian dinosaurs. They were small-to-medium size but well-provided with weapons, including a long sickle claw on the hind feet that may have been used to disembowel or grasp prey. Global distribution, Middle Jurassic to Late Cretaceous.

Dromaeosaurus a genus of theropod ornithischian dinosaurs in the family Dromaeosauridae. Only 7 feet long and weighing just over 30 pounds, it was a small carnivore. Known only from fragments, it has been reconstructed in museum casts from what is known of other dromaeosaurids. North America, Late Cretaceous, 77–75 Ma.

Dromiceiomimus a possible genus of bird-like dinosaurs of the Late Cretaceous, generally considered synonymous with ***Ornithomimus****, q.v*.

Dromomeron a genus of non-dinosauriform dinosauromorphs in the family Lagerpetidae. Known from three fragmentary specimens from New Mexico and Argentina that indicate bipedality, it was lightly built, about 3 feet long and undoubtedly a fast runner. Late Triassic, 220–212 Ma.

Dromiciops gliroides an extant species of small marsupials in the superorder Australidelphia; called locally *monito del monte*. Mouse-like, it is 6–10 inches long (half of it the tail) and has a diet of insects and occasional fruits. Known only in central Chile, it is a relict, the only extant American representative of the great group of Australasian marsupials. How it came to South America is a matter of dispute.

Dromornithidae a family of gastornithiform ratite birds that inhabited Australia between 25 Ma and 30,000 years ago.

Flightless and weighing up to 1000 pounds, they were larger than moas, and *Dromornis stirtoni* was taller than the elephant birds of Madagascar (see ***Aepyornis*** and ***Vorombe***) but probably not quite so heavy. The family also includes *Barawertornis, Bullockornis, Libandornis,* and *Genyornis*. Australia, Oligocene to late Pleistocene.

Drotops armatus a heavily armored species of phacopid trilobites in the family Phacopidae. It was 8 inches long and is distinguished especially by many stout

spines in rows from its eye ridges back along the entire thorax. Morocco, Middle Devonian, 388–384 Ma.

Dryolestidae a family of small pantothere eutherian mammals; North America and Europe, Middle Jurassic to Late Cretaceous.

Dryopithecus "oak-ape," a genus of monkey-like primates in the family Hominidae. About 4 feet long, it closely resembled modern orangutans in its long arms, short legs, and curved fingers. Asia, Africa, and Europe; late Miocene, 12–9 Ma.

Dryosaurus a genus of ornithopod dinosaurs in the family Dryosauridae. It was bipedal and herbivorous, with a five-fingered manus. Known only from juvenile specimens between 8 and 14 feet long, *Dryosaurus* adults were probably less than 20 feet long. Western United States and Europe, Late Jurassic, 151–145 Ma.

Dryptosaurus a genus of primitive tyrannosaurid dinosaurs. Known definitively from a partial skeleton of one individual, it is estimated to have been as much as 25 feet long. Named "tearing lizard" by E.D. Cope because of the 8 inch claws on at least one of the three digits on its forelimbs, it is the only known large carnivorous dinosaur of Eastern North America. Late Cretaceous, 67 Ma.

Dunbarella a genus of thin-shelled pectinoid bivalves in the family Pterinopectinidae. Up to 1.5 inches wide and flattened except for a low beak, it had numerous radial ribs and faint concentric lines of ornamentation. It sometimes is found in association with ammonoids, which undoubtedly preyed on it. North and South America, Europe, and Asia; Carboniferous to Permian.

Dunbaria a genus of pterygote insects in the order Palaeodictyoptera. It had sucking mouth parts and dragonfly-like wings with a wingspan of 1.25 inches. A specimen from Kansas shows veins and color bands in the wings. United States and Russia, early to middle Permian.

Dunkleosteus a genus of very large arthrodire placoderms in the suborder Brachythoraci, originally named *Dinichthys terrelli*. One of many armored fish that became extinct at the end of the Devonian, *Dunkleosteus,* grew at least 20 feet long and weighed more than a ton, with some estimates much higher. Its posterior skeleton has not been preserved, probably because it was cartilaginous. Armed with very powerful jaws and bony plates instead of teeth, it preyed upon many marine animals. Cosmopolitan, Late Devonian.

Durophagy see **Mesozoic Marine Revolution,** ***Dapedium***, and ***Globidens***.

Dusignathus seftoni **Deméré** a subspecies of Pleistocene walrus intermediate between its terrestrial ancestors and later walruses. It is characterized especially by a large bone crest on its head and short, tusk-like canine teeth. It is 1 of 24 species

of walruses that evolved from bear-like land animals since the late Oligocene, with *Odobenus* being the only surviving species; see also ***Valenictus***. Southern California, 3 Ma.

Dyticonastis a monospecific genus of amphisbaenian reptiles. A burrowing limbless lizard, *D. rensbergeri*, is known only from sites in Central Oregon and is the only known amphisbaenian west of the Rocky Mountains. United States, late Oligocene to early Miocene.

E

East Kirkton Quarry a site of importance to the paleontology of Romer's gap. A former limestone quarry, it has yielded since the 1980s skeletal fossils of tetrapods and other Carboniferous animals such as the temnospondyl *Balanerpeton*. See also ***Silvanerpeton***. Scotland, Early Carboniferous, 435 Ma.

Echinerpeton intermedium a poorly known species of early synapsids, it is known only from fragmentary remains found in Nova Scotia, and its relationship to other synapsids is unclear. Nevertheless, it may be the earliest-known synapsid, dated between 311 and 308 Ma. One of the specimens seems to have borne high neural spines similar to those of the pelycosaurs. See also ***Archaeothyris***. Canada, Middle Pennsylvanian, 315–307 Ma.

Echinocorys a genus of irregular burrowing euechinoids in the family Holasteridae. It was atelostomate and generally subconical with a flattened base; the ambulacra were flush, giving it a smooth surface. North America, Europe, and Asia; Late Cretaceous to late Paleocene.

Echinocystitoida an order of early echinoids in the subclass Perischoechinoidea. Poorly known, it includes the families Echinocystitidae and Lepidesthidae and a few other scattered genera. Europe and United States, late Silurian to late Permian or Early Triassic.

Echinodermata "spine skin," a phylum of marine, mostly benthic animals known definitively from the late Ediacaran to the present, with about 7,000 extant and 13,000 extinct named species. The largest phylum with no terrestrial or freshwater representatives, it is characterized by a rough or spiny skin, pentameral radial symmetry, a water vascular system, and an internal skeleton of calcareous plates. The phylum includes principally starfish (Asteroidea), brittle stars (Ophiuroidea), sea urchins and sand dollars (Echinoidea), sea cucumbers (Holothuroidea), and sea lilies (Crinoidea). Extinct classes of echinoderms are the Blastoidea, Cyclocystoidea,

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Cystoidea, Diploporita, Edrioasteroidea, and Paracrinoidea. A subphylum called Eleutherozoa has been proposed to include all echinoderms except the Crinoidea.

Echinoidea the sea urchins and sand dollars, a class of echinoderms in the subphylum Echinozoa. Echinoids are characterized by a generally spherical or subspherical shape except in some irregular groups, especially the flattened sand dollars (Clypeasteroida). Echinoids are typically spiny and, like all echinoderms, have pentameral symmetry, with tube feet protruding from pores in the five ambulacra. They have moveable appendages and a skeleton of interlocking calcareous plates. Most have a feeding apparatus called the lantern, which is composed of five pyramidal plates, each with a single calcitic tooth; those without the feeding lantern are referred to as atelostomate. While all Paleozoic echinoids are regular, many later families are irregular. Echinoids typically have an anal area (periproct) in the upper surface; in regular genera the periproct is in the center, while in irregular genera, it is located away from the center. Global distribution, Middle Ordovician to Recent.

Echinoneoida an order of irregular echinoids established in 2010 to include the Conuloidea, Echinoneidae, *Cluniaster*, and *Mattsechinus*. North and South America, Europe, and Asia; Early Cretaceous to Pliocene, 136–4 Ma.

Echinosphaerites a genus of cystoid echinoderms in the class Cystoidea. Spherical and 1–2 inches wide, it has a mesh skeleton of radiating sparry calcite crystals with a smooth surface. North America, Eurasia, and North Africa; late Cambrian to Late Ordovician.

Echinothurioida an extant order of deep-water euechinoids, perhaps the earliest of the modern echinoids. Closely related to the earlier Pedinoida and Diadematoida, they had hollow spines and a flexible test. Cosmopolitan but mainly Europe, Middle Jurassic to Recent.

Echioceratidae a family of ammonitid ammonoids in the superfamily Psiloceratoidea. They are evolute, strongly ribbed, and generally 2 inches wide. *Echioceras raricostatum* is an index fossil in the Early Jurassic. Global distribution, Early Jurassic, Sinemurian, 197–190 Ma.

Echolocation the ability to locate objects by biological sonar, emitting squeals or clicks and using the reflection of the sound to measure the size and location of the object. Echolocation is notable terrestrially in bats and used to a lesser extent by some birds and small mammals. In marine environments, it was first developed in the Eocene by odontocete whales and became widespread in dolphins and porpoises of the Miocene.

Ecphora a large genus of predatory snails in the family Muricidae. The name "bearing out" is an architectural term going back to Vitruvius and refers to the

distinctive T-shaped ribs protruding from the spiral shell. Germany and Eastern United States, late Eocene to Pliocene.

Edaphosaurus "pavement reptile," a genus of pelycosaurian synapsid reptiles in the family Edaphosauridae. Perhaps the earliest large terrestrial herbivore, it is named for thick clusters of teeth in both the lower and the upper jaws. It is also notable for the showy sail that more than doubled its skin surface, extending upward along its backbone on almost two dozen long, curving neural spines more than 2 feet long. *Edaphosaurus* was smaller than some of its spenacodontid cousins, such as the even more spectacular *Dimetrodon*. United States and Europe, late Pennsylvanian to early Permian.

Edentates see **Xenarthra**.

Edentulous lacking teeth.

Ediacara Conservation Park an important Ediacaran site **in** the Flinders Ranges of South Australia. It was greatly enlarged in 2018 by the acquisition of a large parcel of the Nilpena cattle station. Now proposed as a World Heritage Site because of its exceptional preservation of fossils from near the end of the Proterozoic, it is especially important for areas as large as several hundred square feet where undisturbed fossil assemblages are exposed, making reconstruction of ecological communities possible. Australia, late Ediacaran, 570–560 Ma.

Ediacaran the final period of the Precambrian Eon and Neoproterozoic Era, 635–541 Ma, formerly called Vendian. See also **Geologic Time Scale.**

Ediacaran biota a general term for late Precambrian assemblages of primitive organisms first found in the Ediacara Hills (in the Flinders Ranges of Northern South Australia) and later worldwide. Very difficult to identify and classify, they are mostly impressions in overlying strata. The Ediacarans include a great variety of multicellular organisms, some of which are thought possibly ancestral to sponges, jellyfish, corals, worms, mollusks, and brachiopods. Most of them, however, have no eyes, mouth, gut, anus, or other metazoan features. Several of the Ediacarans seem likely to be evolutionary dead ends that are unrelated to later taxa, but some of the world's current animal body plans may have originated in the Ediacaran. Almost all other current body plans are represented in the great radiation of species at the beginning of the Cambrian.

Edmontosaurus a genus of late Maastrichtian hadrosaurs, duck-bill dinosaurs in the subfamily Saurolophinae; synonym *Anatosaurus*. With a short neck but almost 40 feet long, some were among the largest hadrosaurids. Well-preserved skeletons of one species, *E. annectens*, show skeletal articulation and skin impressions. One was originally named *Trachodon annectens* and referred to as the "*Trachodon*

mummy" because of its skin impressions and complete skeleton; and another called "Dakota," found in 1999, shows possible stripes on its fossilized skin. Although widespread across Western North America, *Edmontosaurus* was first discovered in the Horseshoe Canyon Formation of Southern Alberta. See also ***Ugrunaaluk***. North America, Late Cretaceous, 74–66 Ma.

Edrioasteroidea a long-lived class of stemless crinozoan echinoderms. Among the earliest echinoderms, they may have given rise to the crinoids in the Ordovician. They were obligately encrusting on hard substrate or on other organisms, such as brachiopods and conulariids. Edrioasteroids generally have ambulacra that are sometimes curved and sometimes spiral. Although never numerous, they survived from the early Cambrian (possibly the Ediacaran) to the middle Permian. Global distribution.

Effigia a famous example of convergent evolution, a genus of crocodylomorph archosaurs in the family Shuvosauridae. It was 6–8 feet long, edentulous but omnivorous, and primarily bipedal, closely resembling the theropod ornithomimosaurian dinosaurs of the Early Cretaceous. But close examination showed that, like its close relative *Shuvosaurus*, it was more closely related to crocodilians. New Mexico, Late Triassic, 210–205 Ma.

Efraasia a genus of basal sauropodomorph dinosaurs. Known mainly from juvenile skull and skeletal fragments found in Germany in the early twentieth century, *Efraasia* has had a contentious history. Its name has settled as *E. minor*, and its diet is now thought to be only herbivorous, but whether it was bipedal or quadrupedal is still unclear. It was about 20 feet long and bears some theropod traits but is more closely related to the Guaibasauridae, *Saturnalia*, and *Buriolestes*. Germany, Late Triassic, 211 Ma.

Egg Mountain a well-known site of a purportedly colonial dinosaur nesting ground in the Two Medicine Formation of Montana, where the first dinosaur eggs in North America were found. The site is notable especially for the *Maiasaura* nests with numerous eggs and possible indications of dinosaur parenting behavior. There are also specimens of *Orodromeus* and *Troodon*, as well as *Troodon* eggs. Late Cretaceous, 84–75 Ma.

Eileanchelys a genus of early turtles known only from partial specimens found in Scotland. About a foot long and low-domed, it is similar to the Early Jurassic *Kayentachelys*. Middle Jurassic, 164 Ma.

Einiosaurus "bison lizard," a monospecific genus of medium-sized ceratopsid dinosaurs in the subfamily Centrosaurinae. From 15 to 20 feet long and weighing about 2 tons, *E. procurvicornis* looked like a small *Triceratops* except for a downward-curving horn extending forward from its nose. It is known from a dozen

individuals, all from the Two Medicine Formation in Montana. United States, Late Cretaceous, 75–73 Ma.

Elaphrosaurus a genus of theropod dinosaurs in the family Noasauridae, broadly similar to the ornithomimids of the Cretaceous. About 20 feet long, it had a long and slender trunk; no skull is known, and it may have been omnivorous. Tanzania and possibly United States, Late Jurassic.

Elasmobranchii "plated gills," a subclass of chondrichthyan fish that includes the Batoidea (skates, rays, and sawfish) and the Selachii (sharks). They have small scales on the skin surface and five to seven pairs of gills with exposed slits. Global distribution, middle Silurian to Recent.

Elasmosauridae a later, highly specialized group of plesiosaurs, notable especially for a very long neck. The type species *Elasmosaurus* at 46 feet was the longest-known plesiosaur. Global distribution, Early to Late Cretaceous.

Elatocladus a genus of conifer trees in the family Podocarpaceae. Widespread in the tropics from the Permian through the Jurassic, it seems to be known in the Cretaceous only from colder sites. Global distribution, late Permian to Late Cretaceous.

Eldredgeops a famous species of trilobites in the order Phacopida and family Phacopidae; originally named *Phacops rana*. From 2 to 3 inches long, it is notable for its very large, schizochroal eyes and the warty surface of its inflated, semicircular glabella. North America and Morocco, Middle Devonian.

Electrorana limoae a species name given collectively to four partial frog specimens in amber described in 2018. Burma, Early Cretaceous, 99 Ma.

Elephant birds see ***Aepyornis*** and ***Vorombe***.

Elephantidae the elephants and mammoths, an extant family of large proboscidean mammals that split off from mastodons and the other proboscideans in the Pliocene and spread throughout the Northern Hemisphere. They are represented today by two monospecific genera, which are slightly smaller than some of the Pleistocene genera. See also **mammoths** and **Mammutoidea**. North America, Europe, Asia, and Africa; late Eocene to Recent.

Elginerpeton a monospecific genus of early tetrapods, intermediate between fish and amphibians. *E. pancheni* was found in Upper Frasnian strata and dated at 375 Ma, 10 million years earlier than *Ichthyostega*. Known from humerus, tibia, and jaw bones, it was about 5 feet long. Scotland, Late Devonian.

Ellesmeroceras a genus of small nautiloid cephalopods in the order Ellesmerocerida. The shell is usually orthoconic but may also be curved. North America and Asia, late Cambrian to Early Ordovician.

Elliot Formation a rock formation in South Africa that has produced many sauropodomorph specimens, such as *Massospondylus* and *Melanorosaurus*; Late Triassic to Early Jurassic.

Ellisdale deposits an important Late Cretaceous Konzentrat-Lagerstätte in New Jersey. Thought to have resulted from a single coastal storm event, the site has become the most important source of middle Campanian fossils on the East Coast of North America, representing marine, coastal, and terrestrial ecosystems. The more important fossils include dozens of fish and other marine taxa; several dinosaurs, especially ornithopods and theropods; several amphibians, reptiles, and mammals; and several species of plants. The distinctive makeup of the land fauna seems to support the idea that Appalachia constituted an isolated fauna, with little or no interchange of species with other areas of North America. United States, Late Cretaceous, 80–76 Ma.

El Montsec Lagerstätte a site in Catalonia that has produced many fossils from the beginning of the Cretaceous, about 130 Ma, slightly earlier than the better-known Las Hoyas site of Eastern Spain. El Montsec is known for the only specimen of *Noguerornis*, several important specimens of early orb-weaving spiders, and many beetles and other insects. Spain, Early Cretaceous.

Elrathia kingi a genus of medium-sized trilobites in the order Ptychopariida. Oval and 1–2.5 inches long, it had a semicircular cephalon with a short, blunt glabella. It is one of the most common trilobites of North America, commercially exploited especially from the Wheeler Shale Formation of Utah. North America, Europe, and Asia; middle Cambrian.

Embolomeri a contentious suborder of large, primitive fish-eating anthracosaurian amphibians. Although they have some reptilian features, they are probably not ancestral to reptiles. The embolomeres evolved from reptiliomorph amphibians in the Early Carboniferous, developing vertebral adaptations that facilitated undulatory swimming. They survived the end-Permian extinction and may have partially adapted to terrestrial life before becoming extinct. North America and Europe, Carboniferous to Early Triassic.

Embrithopoda "heavy-footed," an order of large paenungulate eutherian mammals, represented mainly by genera of the Paleocene and Eocene but known best by the latest embrithopod, ***Arsinoitherium***, *q.v*. Despite their resemblance to the

rhinoceros, the Embrithopoda are more closely related to elephants. Africa, Asia, and Europe; late Paleocene to early Oligocene.

Emeidae a family of Moas; see **Dinornithidae**.

Emu Bay Shale an early Cambrian formation on Kangaroo Island. Somewhat earlier than the Burgess Shale and Chengjiang sites, the Emu Bay Shale has produced several fossils similar to those of the more famous Lagerstätten, including *Anomalocaris* and *Tuzoia*, as well as many trilobites and other arthropods. Its coarse-grained strata were deposited in relatively shallow water, so that the degree of preservation is lower. South Australia, early Cambrian, 520 Ma.

Emuellidae a family of early trilobites in the order Redlichiida. They are characterized generally by an elongated body with numerous thoracic segments and by long genal and pleural spines. Australia and Antarctica, early Cambrian, 520–516 Ma.

Enaliarctos a genus of stem-pinnipeds in the superfamily Otarioidea, probably ancestral to the desmatophocids. It had a short tail and retained the carnassial teeth of its terrestrial ancestors (possibly related to the ursids) but had flipper-like limbs, probably webbed. See also ***Puijila***. North America, late Oligocene to early Miocene 24–22 Ma.

Enaliornis "sea bird," a genus of hesperornithine birds in the small family Enaliornithidae. The type of genus *Enaliornis* is the oldest-known hesperornithine, dated between 100 and 94 Ma, near the beginning of the Late Cretaceous (Albian). Known from three partial skulls and many bone fragments, *Enaliornis* was about the size of a large pigeon. A foot-propelled diver that probably nested near water, it was originally named *Pelagornis* but is not closely related to that bird of the Miocene. England, Late Cretaceous.

Enantiornithiformes an order of birds in the clade Enantiornithes, known only from the Cretaceous. These "opposite birds" (called so because the articulation of the shoulder bones is the reverse of the articulation in modern birds) seem to have originated in the Early Cretaceous and to have achieved global distribution toward the end of the period. They may have been the predominant type of bird during the Cretaceous, but they were all extinguished in the crisis that marked the end of the Mesozoic era. The Enantiornithiformes were more advanced than Jurassic birds in having enlarged breast bones, shortened tails, and a pygostyle; but they were less similar to modern birds than were later genera such as *Ichthyornis* and *Hesperornis*. The sparrow-sized *Iberomesornis* (Spain, Early Cretaceous, 125 Ma) had a pygostyle but with a claw on each wing was one of the most primitive of the group.

The type of genus *Enantiornis* (Argentina, Late Cretaceous, 70 Ma) was more advanced and seems to have been a good flyer. See also ***Eoenantiornis*** and **amber**. South America, Spain, and China; Early to Late Cretaceous.

Enchodus a genus of salmoniform neopterygian fish in the family Enchodontidae. Up to 5 feet long and weighing 25 pounds, *E. petrosus* was a predatory fish with fangs more than 2 inches long; seven other species were smaller. Global distribution, Late Cretaceous to early Eocene.

Encrinida an order of stalked crinoids of the Triassic. The 2015 discovery *Baudicrinus* is probably the earliest encrinid (251 Ma); they are well-known from the Middle and Late Triassic. Cosmopolitan, Early to Late Triassic.

Encrinidae a family of pelmatozoan crinoids in the order Encrinida. They are generally tulip-shaped and attached to the substrate by a long stalk, usually found in an unopened position. Some Triassic formations are dominated by accumulations of encrinid stalks. Cosmopolitan, Middle to Late Triassic.

Encrinus a genus of stalked crinoids in the family Encrinidae. It is characterized by its tulip shape, with a large cup 1–2 inches long at the top of a long, circular stalk covered with regular ossicles. The stem did not have cirri, and it is unclear whether it had a holdfast. Europe, Asia, New Zealand, and North America; Middle Triassic.

Encrinurus a widespread genus of trilobites in the order Phacopida and family Encrinuridae. It is characterized by the large tubercles on its headshield which give it the appellation of "strawberry-headed." Global distribution, Middle Ordovician to Early Devonian.

Endoceratidae a family of large, straight-shelled nautiloid cephalopods in the order Endocerida. The family includes possibly the largest-known Paleozoic fossils, specimens of the giant *Cameroceras* reaching a length of 20–25 feet. Global distribution, Early Ordovician to Early Devonian.

Endothyroidea an extinct superfamily of large benthic foraminiferans in the order Fusulinida, frequent index fossils in the Late Devonian and Early Carboniferous; global distribution, Devonian to Late Triassic.

Enhydra a genus of sea otters, marine mammals in the suborder Caniformia and family Mustelidae. Appearing in the sea much later than the pinnipeds, the earliest sea otter is *E. reevei* of the late Pliocene and early Pleistocene. The only other extinct species is *E. macrodonta*, known only in the late Pleistocene. Europe and United States.

Ensifera the crickets and katydids, a suborder of stridulatory chewing insects in the order Orthoptera. The Ensifera were among the earliest flying insects; global distribution, Late Carboniferous to Recent.

Enteletes a genus of rhynchonellate brachiopods in the order Orthida and superfamily Enteletoidea. About half an inch long and an inch wide, it was strongly biconvex, almost globular, with very strong ribbing. Carboniferous to late Permian, with global distribution in Permian.

Enteletoidea a superfamily of rhynchonellate brachiopods in the order Orthida and suborder Dalmanellidina. Up to 1.5 inches wide, their shells are generally biconvex and strongly ribbed. Global distribution, Early Ordovician to Permian or possibly Triassic.

Entelodontidae a family of large, primitive artiodactyl mammals in the clade Cetancodonta and superfamily Entelodontoidea. Although long assigned to the Suina, they are now considered closer to whales and hippopotamuses than to pigs. They had bony flanges or bumps on each side of the jaw, so that they superficially resemble warthogs. North America, Europe, and Asia; middle Eocene to early Miocene.

Entelognathus primordialis a species of placoderm fish with advanced jaw features and other features associated with bony fish. Described in 2013, the 8-inch-long *Entelognathus* suggests a closer relationship between placoderms and osteichthyes than previously thought. China, late Silurian, 423–419 Ma.

Enteropleura a short-lived genus of bivalves in the order Ostreoida and family Halobiidae. Similar to *Daonella* but thin-shelled, *Enteropleura* was widespread in Eurasia and North America in the Middle Triassic, 247–237 Ma.

Enteropneusta the acorn worms, an extant class and order of soft-bodied invertebrates in the phylum Hemichordata. Generally a few inches long, some grow as long as 6 feet. Most families of acorn worms burrow in sediment on the ocean floor, with one deep-sea family, the Torquaratoridae, crawling on the surface of the bottom. One of the best-known enteropneusts is *Saccoglossus*, known from the Carboniferous and still extant in many species. Global distribution, early Cambrian to Recent.

Entognatha an extant class of insect-like arthropods in the subphylum Hexapoda. The wingless Entognatha are so named because they have the mouth parts retracted below the surface of the head. The class includes the Collembola, Protura, and Diplura. Global distribution, Early Devonian to Recent.

Entomoconchacea a superfamily of large myodocopan ostracods in the order Myodocopida, characterized by the absence of a rostrum above the permanent aperture; Europe, Devonian to Permian.

Eoabelisaurus a genus of ceratosaurian theropod dinosaurs in the family Abelisauridae. A bipedal carnivore dated at about 170 Ma, it is the earliest (by 40 million years) and most complete skeleton of an abelisaurid. Patagonia, Middle Jurassic.

Eoalulavis a monospecific enantiornithean genus of birds, the only species being *Eoalulavis hoyasi*. Found at Las Hoyas, it is the earliest-known bird with an alula, a tuft of small feathers attached to the thumb on the forewing, improving maneuverability in flight. Spain, Early Cretaceous, 125 Ma.

Eoandromeda an Ediacaran genus of organisms of an uncertain nature. Circular and up to 1.5 inches wide, they have eight spiral arms that seem to be tubular. Known only from slightly differing specimens from Australia and China, they may be stem-ctenophores, but widely different interpretations have been advanced. 580–550 Ma.

Eobasileus a genus of dinoceratan mammals in the family Uintatheriidae. The largest of the uintatheres, it was the size of a modern rhinoceros at 4 tons, 13 feet long, and 7 feet high at the shoulder. Armed with two short tusks and three pairs of blunt horns, *Eobasileus* closely resembled its cousin, the more widespread *Uintatherium*. United States, middle to late Eocene.

Eocaecilia micropodia a species of caecilian amphibians in the clade Gymnophiona. One of the earliest caecilians, it was about 6 inches long and had eyes and very small limbs. It is known only from one specimen found in Arizona. United States, Early Jurassic, 197–183 Ma.

Eocarcharia dinops a species of large dinosaurs in the family Carcharodontosauridae. It had a massive brow ridge above the eyes, hence its species name, "fierce-eyed." *Eocarcharia* may have been as long as 20–26 feet. Niger, Early Cretaceous, 112 Ma.

Eocene the second epoch of the Cenozoic Era, from 56 to 34 Ma. The earliest orders of modern mammals were present by the end of the epoch, and modern birds diversified throughout. At the end of the Eocene, modern grassland ecosystems had spread, along with modern moths and butterflies as well as the larger grazing mammals. Lower world temperatures occurred toward the end of the period, introducing minor glaciations.

Eocrinidae a family of early stalked crinoids in the class Eocrinoidea and order Gogiida. The makeup of the family is disputed, but, in addition to the generally accepted *Gogia,* the Paleobiology Database includes *Alanisicystis, Globoeocrinus, Guizhoueocrinus,* and *Sinoeocrinus*. Cosmopolitan, Cambrian.

Eocrinoidea a paraphyletic class of pelmatozoan echinoderms in the subphylum Blastozoa. Ancestral to several other classes, the eocrinoids are the earliest-known stalked and arm-bearing echinoderms. Europe, North America, and China; early Cambrian to late Silurian.

Eodalmanitina a genus of phacopid trilobites in the family Dalmanitidae. From 1 to 2 inches long, it is notable for its raised, crescent-shaped, schizochroal eyes. It had more than a dozen thoracic segments and the small pygidium ended in a short spine. Europe, Middle Ordovician, 461–458 Ma.

Eoderoceratidae a family of ammonoids in the order Ammonitida, characterized by an evolute shell and small spines. South and North America, Europe, and Africa; Early Jurassic, between 199 and 183 Ma.

Eodiscina a suborder of trilobites in the order Agnostida. They are isopygous and very small, less than an inch long. Early Eodiscina genera are notable for their abathochroal eyes, but later genera are eyeless. Global distribution, Cambrian to Silurian.

Eodiscoidea a superfamily of trilobites generally considered part of the order Agnostida. See also ***Pagetia***. Global distribution, early to late Cambrian.

Eodromaeus a basal genus of theropod dinosaurs about 4 feet long but weighing only about 11 pounds. Similar to *Eoraptor* but probably not closely related, *Eodromaeus* could probably run at about 20 miles per hour. Argentina, Late Triassic, 231–230 Ma.

Eoenantiornis a monospecific genus of enantiornithean birds known from one specimen found in the Yixian Formation. Dated at the beginning of the Aptian Age, 125 Ma, *E. buhleri* was about 5 inches long. It is one of the most primitive and oldest of the known enantiornithean birds. Jehol biota, China, Early Cretaceous.

Eognathacantha ercainella a possible early species of chaetognaths, known only from a whole-body specimen found in the Maotianshan Shales; China, early Cambrian, 520 Ma.

Eohippus a genus of perissodactyl ungulates in the family Equidae. Formerly synonymous with *Hyracotherium*, it is now considered a separate monospecific genus. *Eohippus angustidens* was the size of a medium-sized dog. North America, early Eocene.

Eolacertilia a clade of lepidosauromorph reptiles. It is generally considered to contain *Paliguana* and the Kuehneosauridae, and in 2014 *Megachirella* was suggested as a member. Several other taxa, such as the Tanystropheidae, have been reclassified. Cosmopolitan, known from the United States, Europe, and South Africa; Early to Late Triassic.

Eolorica deadwoodensis a species of loriciferan animals discovered in an outcrop of the Deadwood Formation in Saskatchewan in 2017. Canada, middle Cambrian.

Eolympia see **Ceriantharia.**

Eomaia scansoria an enigmatic species of early mammals. Dated at 125 Ma and known from one complete skeleton, it was only about 6 inches long, nose to tail. Although it had several features common in placental mammals, including fur, it lacked several other features common to all placentals. It also had an epipubic bone, a marsupial character. Jehol biota, China, Early Cretaceous, 125 Ma.

Eomanis a genus of pangolins in the suborder Eupholidota. The earliest-known pangolin from Europe, it was only 20 inches long and had scales only on the body and not on tail or legs. Messel Shale Pit, Germany; early Eocene.

Eomoropidae a primitive family of perissodactyl ungulate mammals in the suborder Ancylopoda, related and possibly ancestral to the chalicotheres. Although they bore claws on their feet, they were sheep-sized grazers or browsers. Asia and North America, early Eocene.

Eomyidae a family of rodents in the suborder Castorimorpha and superfamily Geomyoidea. The family includes the earliest gliding squirrel (*Eomys quercyi*) and a variety of small- and middle-sized genera. North America, Europe, and Asia; middle Eocene to Pleistocene.

Eophalangium see **Opiliones**.

Eophrynus a genus of spider-like arachnids in the order Trigonotarbida. It is characterized by numerous dorsal knobs and half a dozen ventral ridges and was unable to spin silk. Europe, Late Carboniferous.

Eoraptor lunensis a species of theropods, one of the earliest dinosaurs, dated at 231.4 Ma. Generally considered a primitive saurischian close to the ancestry of both

sauropodomorhs and theropods, *Eoraptor* was lightly built, and the size of a greyhound is about 3 feet long. It was more primitive than other early theropods in having no jaw-hinge, and its degree of bipedality is unclear. It was omnivorous, probably mainly carnivorous, with curved and serrated teeth and three-fingered manus adapted to tearing flesh. Ischigualasto Formation, Argentina, Late Triassic.

Eoredlichia a genus of medium-sized trilobites in the subfamily Redlichiina, probably descended from *Lemdadella*. From 5 to 8 inches long, it had a broad and flattened cephalon, robust genal spines, and a short pygidium. China, early Cambrian.

Eorhynchochelys sinensis a genus of Triassic turtles in the order Testudines. It may be a striking example of mosaic evolution in having a toothless beak but no carapace, although its ribs were broad and flattened. *Eorhynchochelys* was 6 feet long, with a tail longer than its disc-like body. The skull seems to have openings, more evidence that turtles are descended from diapsid reptiles, not from the less-advanced anapsids. China, Late Triassic, 228 Ma.

Eosimias a genus of extremely primitive anthropoid primates, significant because it seems to represent a transitional figure between the higher and lower primates. *Eosimias* is characterized especially by a deep chin and dagger-like canine teeth similar to those of many modern monkeys. Smaller than expected for an intermediate form between the upper and lower primates, it is the size of a shrew; the largest of the four species so far described weighed only 10 ounces. China, middle Eocene, 40–45 Ma.

Eospermatopteris a genus of early cladoxylopsid trees in the order Pseudosporochnales. Long known from trunk and root sections found in life position (the "Gilboa stumps"), *Eospermatopteris* has now been united with *Wattieza*, the crown of the tree. Resembling a large tree fern, it grew to 25 feet high and reproduced with spores, with at least 8 branches covered with whorls of forked fronds. North and South America and Europe, Middle to Late Devonian.

Eospirifer a genus of spiriferid brachiopods in the family Cyrtiidae. Articulate and biconvex, E*ospirifer* grew up to 1.3 inches and is characterized by a broad fold, very fine ribs, and spiral brachidia. Global distribution, Middle Ordovician to Middle Devonian.

Eosuchia a polyphyletic group formerly considered an order of diapsid reptiles, not related to the gharial *Eosuchus* and now discarded except as an informal term. Once considered numerous, the "eosuchians" are now restricted to the small neodiapsid family **Younginidae**, *q.v.* South Africa and Madagascar, Permian to Triassic.

Eosuchus lerichei an early genus of crocodylomorphs, generally considered a stem-gharial in the order Crocodilia and superfamily Gavialoidea. Similar to the

modern *Gavialis*, *Eosuchus* is well-known from Europe and the United States and possibly from Thailand. Late Paleocene to late Eocene.

Eotarbus see ***Palaeotarbus***.

Eothele see ***Palaeothele*.**

Eotitanops a genus of brontotheres, perissodactyl grazing mammals. The earliest accepted brontothere, *Eotitanops* was less than 2 feet high and resembled a small modern tapir. It had five digits on the manus and three on the pedes. United States and Asia, early to middle Eocene.

Eotitanosuchus a genus of basal therapsids, placed tentatively in the suborder Biarmosuchia although significantly different from other biarmosuchians. Known from a single partial skull found near specimens of *Biarmosuchus* and *Estemmenosuchus*, it is estimated to have been about 9 feet long. Russia, middle Permian, 267 Ma.

Eotragus a genus of early ruminants in the family Bovidae. About 40 pounds and bearing two vertical horns, *Eotragus* was the size of a gazelle and browsed in open and wooded grasslands. The earliest well-known bovid, it evolved in Eurasia around 20 Ma and appeared in Africa soon afterward. Asia, Europe, and Africa; early to late Miocene.

Eotyrannus a genus of early theropod dinosaurs in the superfamily Tyrannosauroidea. Poorly known but estimated at about 12 feet long, it was small and gracile and similar to other early tyrannosauroids such as *Dilong* and *Guanlong*. England, Early Cretaceous, 130 Ma.

Eozostrodon a contentious genus of early cynodont mammals tentatively placed in the family Morganucodontidae. Estimated at 4 inches long, it is known only from disarticulated fragments, mainly teeth, it is considered by some to be synonymous with *Morganucodon*. Found in England near the boundary of the Triassic and Jurassic.

Ephemeroptera the mayflies, an extant order of palaeopteran insects. Smaller and more slightly built than the Anisoptera, their dragonfly cousins, they have smaller hindwings and long cerci extending behind a relatively short abdomen. Like the Anisoptera, they are notable for the primitive characteristic of wings that cannot be folded over the abdomen. The earliest mayfly is *Lithoneura*, known from the Late Pennsylvanian Mazon Creek assemblage, and many ephemeropteran specimens are known from the Permian and Jurassic. Global distribution, Late Carboniferous to Recent.

Epidendrosaurus a genus of sparrow-sized saurischian dinosaurs in the suborder Theropoda; synonym *Scansoriopteryx*. It is notable for the extreme elongation of the forelimb digits and other adaptations to a tree-dwelling habit. China, Late Jurassic, 160 Ma.

Epifaunal referring to benthic animals living on the surface of the seafloor or a lake bed, either attached or free moving, as opposed to infaunal organisms, which construct burrows or tubes in the bottom sediment.

Epigaulus see ***Ceratogaulus***.

Epi-planktic of marine organisms attached permanently to a floating substrate.

Epithyris a genus of articulate terebratulid brachiopods in the family Postepithyrididae. It has a short loop, and its shell is punctate. Europe and Africa, Middle to Late Jurassic.

Eporeodon a genus of oreodonts in the family Merycoidodontidae and subfamily Eporeodontinae. Probably related to camels, it was an herbivorous artiodactyl with four digits, weighing 200–300 pounds. Not numerous and restricted to Western North America, early Oligocene to early Miocene.

Equidae the horses, a family of perissodactyl mammals in the suborder Hippomorpha and the superfamily Equoidea. The palaeothere *Hyracotherium*, from the middle Paleocene, was long considered the first horse, but it is no longer considered ancestral to the Equidae. The earliest unquestioned Equidae are *Eohippus* and *Protorohippus*, fox-sized animals of the early Eocene. Early horses increased in size very slowly from the late Paleocene to the late Oligocene, then diversifying rapidly in the early and middle Miocene. From the late Miocene to the Pleistocene, their size continued to increase, with smaller species becoming extinct. The line of descent of the later Equidae is well-documented, from *Miohippus* (Oligocene), *Hypohippus* (Miocene), *Merychippus* (Miocene), and *Dinohippus* (Miocene to Pliocene) to the earliest-known species of the genus *Equus, E. simplicidens* (late Pliocene to Pleistocene). *Equus* quickly migrated to Eurasia and Africa but became extinct in North America about 12,000 years ago.

Equisetum a genus of horsetails in the class Equisetopsida. It appeared in the Devonian and became widespread in the Carboniferous; there are about 25 extant species of *Equisetum*. Global distribution, Devonian to Recent.

Equisetopsida an extant class of plants now considered a relative of the ferns and assigned to the Filicopsida. It was formerly called Sphenopsida or Sphenophyta. Global distribution, Late Devonian to Recent.

Eramosa Lagerstätte a fossil locality in Ontario, Canada, that has produced well-preserved autochthonous specimens of eurypterids and other arthropods, annelid worms, conodonts, and fish from the middle to late Silurian.

Erbenochile an unusual genus of phacopid trilobites in the family Acastidae. About 2 inches long, *Erbenochile* is especially notable for its two eye columns, 1 inch high with a brim (a palpebral lobe) overhanging the top. Each eye had up to 500 lenses, and the largest species had 360-degree vision. *Erbenochile* was spinose, with median spines on the thorax and pygidium as well as spines on all fringes, including the pygidium. North Africa, Early to Middle Devonian, 403–393 Ma.

Eremotherium a genus of large ground sloths in the subfamily Megatheriinae. From 18 to 20 feet long and weighing 3 tons, it could sit at least partially erect. Almost toothless, it was unusually sexually dimorphic, males being almost 50% larger than females. It appeared about 5 Ma and became extinct about 11,000 years ago. North and South America, Pleistocene.

Eretmorhipis carrolldongi a species of marine neodiapsid reptiles in the order Hupehsuchia. It had the typical small skull, dorsal osteoderms, gastralia, and long tail of hupehsuchians, but its name reflects its larger than usual, fan-shaped, paddle-like limbs. China, Early to Middle Triassic.

Erinaceidae the hedgehogs and gymnures, a eulipotyphlan family of small mammals. For extinct erinaceids see ***Amphechinus, Deinogalerix***, and ***Silvacola*.**

Eritherium a proposed genus of proboscideans described in 2009, considered a basal proboscidean. Much earlier than *Moeritherium* (late Eocene) and other ancestral proboscidean genera, it is known only from a partial skull, jaw, and teeth. Morocco, Paleocene, 60 Ma.

Ernietta plateauensis a species of enigmatic Ediacaran organisms, probably related to ***Pteridinium***, *q.v.* It is known in several forms that have been given species names but probably represent different life stages. Namibia, late Ediacaran, 550 Ma.

Eryon a genus of small decapods in the family Eryonidae. Well-known from the Solnhofen quarry, *Eryon* resembles a crab-headed lobster. About 4 inches long, it has a broad carapace and short tail. Europe, Early to Late Jurassic.

Eryops "drawn-out face," a monospecific genus of semi-aquatic temnospondyl amphibians in the family Eryopidae. Perhaps the largest land animal of its time at 5–10 feet long and 200 pounds, *Eryops* is one of the best-known temnospondyls. Its muzzle is almost as long as that of an alligator, and its ribs are unusually short and straight. United States and Germany, Late Pennsylvanian to early Permian.

Erythrosuchus a genus of archosaurian reptiles in the family Erythrosuchidae, close to the ancestry of the last common ancestor of the archosaurs. At 16 feet long, *Erythrosuchus* was one of the largest predators of the Middle Triassic, competing with therapsids in Southern Africa in the period of time before they disappeared. Restricted to Southern Africa, 250–230 Ma.

Essexella see **Scyphozoa**.

Estemmenosuchus a genus of large dinocephalian therapsids. Known from many complete and partial skeletons, *Estemmenosuchus* was probably omnivorous and is estimated at between 10 and 14 feet long. It is notable for several sets of horns protruding upward and outward from the skull, giving it its name, "crown crocodile." Russia, middle Permian, 267 Ma.

Euarchonta a proposed grouping of primates, tree shrews, (Scandentia), colugos (Dermoptera), and the extinct Plesiadapiformes. Formerly called Archonta, it included bats, which are now considered closer to the Laurasiatheria. Early Paleocene to Recent.

Euarchontoglires one of the four large clades generally considered to comprise the Eutheria, along with the Laurasiatheria, Afrotheria, and Xenarthra. The Euarchontoglires include the Euarchonta, Rodentia, and Lagomorpha. Early Paleocene to Recent.

Eucoelophysis a genus of dinosauriform reptiles tentatively placed in the Silesauridae. About 4 feet long, it is dated around 206 Ma and seems to have some features associated with dinosaurs. United States, Late Triassic.

Eucynodonts the clade of cynodont therapsids that includes the ancestors of mammals; global distribution, Early Triassic to Recent.

Euechinoidea a subclass of echinoids that includes all post-Paleozoic echinoids. Appearing in the Triassic, the euechinoids have diversified and spread worldwide, achieving their greatest diversity in the Holocene. Global distribution, Late Triassic to Recent.

Eugeneodontida an order of holocephalic fish. Distinguished by a tooth-whorl of sharp teeth in the lower jaw, they are poorly known although numerous and worldwide from the Early Carboniferous to the Early Jurassic.

Euhoplites "well-armed," a genus of small ammonitid ammonoids. Its shell had especially strong ribbing and was covered with tubercles and other bumps. North and South America and Europe, Early Cretaceous, 110–100 Ma.

Euhoploceras see ***Sonninia***.

Eukaryota the domain of organisms whose complex cells have a distinct nucleus surrounded by a membrane. They range from microscopic amoebae to the largest plants and animals. Although the oldest eukaryote fossils are about 1.7 billion years old, genetic evidence points to an age of about 3 billion years. See also **Archaea** and **Bacteria**.

Eulipotyphla a clade of small insectivorous mammals that became widespread toward the end of the Cretaceous and is still represented by the shrews, hedgehogs, and moles. See, for example, **Zalambdalestidae** and **Asioryctitheria**. Global distribution, Late Cretaceous to Recent.

Eumalacostraca the subclass of crustaceans that includes most of the modern crustaceans, such as crabs, lobsters, shrimp, crayfish, and sow bugs; global distribution, Cambrian to Recent.

Eumorphotis a genus of scallop-like bivalves in the family Heteropectinidae. It is one of the disaster taxa that survived the Permian extinction and flourished in the Early Triassic. See also ***Claraia***. Global distribution, late Permian to Early Jurassic.

Eunotosaurus a genus of broad-bodied reptiles that may be an intermediate form between turtles and their Paleozoic ancestors. Known from relatively rare but well-described specimens, they had a wide body with several flattened ribs and turtle-like vertebrae. See also ***Pappochelys*** and ***Kayentachelys***. South Africa, middle to late Permian.

Euomphalina an important large group of early gastropods, variously considered an order or suborder. Long placed in the "Archaeogastropoda," they are now being reclassified but are generally thought to include the superfamilies Euomphaloidea, Macluritoidea, Ophiletoidea, and Platyceratoidea. Global distribution, Cambrian to Recent.

Euomphalus a widespread genus of marine gastropod mollusks in the family Euomphalidae; synonym *Straparollus*. Generally about 2 inches wide, the closely coiled shell is usually planispiral but occasionally has a slightly raised spire; it resembles a flattened ammonoid shell. Global distribution, Silurian to Early Cretaceous.

Euoplocephalus tutus a species of large ankylosaurian dinosaurs in the subfamily Ankylosaurinae. Similar in many details to *Anodontosaurus* and *Scolosaurus*, it is one of the largest ankylosaurs. From 19 to 20 feet long and weighing more than 2 tons, it had a very broad pelvis (6 feet wide) and was also 6 feet tall. It had an erect posture and was well-armored with scutes and a large tail club. Southern Alberta, Canada, Late Cretaceous, 76–75 Ma.

Eupantotheria a general term for a group of generally small therian mammals between the Middle Jurassic and the Early Cretaceous, probably including the ancestors of the later marsupials and placentals; they are being reclassified into separate groups.

Euparkeria a genus of primitive reptiles in the possibly monogeneric family Euparkeriidae. Known primarily from the Karoo Basin in South Africa, it is close to the ancestry of the archosaurs. It was about 3 feet long but weighed only 10 pounds and was characterized by recurved teeth, forelimbs slightly shorter than the hindlimbs, and a row of osteoderms down the spine and tail. Africa, Early to Middle Triassic.

Eupodophis a genus of marine snakes in the suborder Serpentes and family Simoliophiidae. Known from only one specimen, a complete skeleton with two almost vestigial hindlimbs, it was about 3 feet long. Lebanon, Late Cretaceous, 92 Ma.

Eurhinosaurus a genus of ichthyosaurs in the family Leptonectidae. Notable for its asymmetrical jaws (similar to those of the modern swordfish), it also had strong front fins and was probably a very fast swimmer. Europe, Early Jurassic, 183–82 Ma.

Europasaurus a genus of small sauropod dinosaurs in the family Brachiosauridae. Estimated at between 5 and 20 feet long, *Europasaurus* seems to represent an example of island dwarfism. Germany, Late Jurassic.

Europejara olcadesorum a species of pterodactyloid pterosaurs in the family Tapejaridae. The oldest tapejarid known and the first found in Europe, it is a relatively small species, with a wingspan of 7 feet. Dated between 130 and 125 Ma, it was discovered in 2012 in a Lower Cretaceous formation in Spain.

Euryalina the basket stars, an extant suborder of ophiuroid echinoderms. Their numerous arms grow up to 2 feet long and can branch in any direction, so that they often resemble a small, bushy plant. They have a poor fossil record; global distribution, Carboniferous to Recent.

Euryapsids a polyphyletic group of early Mesozoic marine reptiles including the ichthyosaurs, noted for a single temporal fenestra near the top of each side of the skull, higher than in the synapsids.

Euryhaline tolerant of a wide range of salinity. Bivalves are more euryhaline than trilobites, which became extinct at the end of the Permian, and also of brachiopods, which have declined since the Paleozoic. Dinoflagellates are also generally euryhaline.

Eurymylidae a family of basal rabbit-like mammals, possibly ancestral to all later rodents; Mongolia, late Paleocene to middle Eocene.

Eurypterida an order of arthropods in the subphylum Chelicerata, commonly called "sea scorpions." They are probably closely related to the Scorpiones but have significant differences. The order contains two suborders, the principal one Eurypterina and the smaller Stylonurina. They had gills, and most were less than 12 inches long, but some were larger than a man (see ***Jaekelopterus*** and ***Pentecopterus***). Eurypterids generally had more than one pair of walking legs, the last of which was larger and used for swimming. They probably gave rise to the Arachnida, which includes the true scorpions, but the horseshoe crab is their closest modern relative. See also **Chimerarachne**. Global distribution, Ordovician to late Permian, 467–252 Ma.

Eurypterus remipes "wide wing oar-foot," the first eurypterid to be discovered and the most common, a species of chelicerates in the family Eurypteridae. It is generally less than a foot long, but individuals as long as 4 feet are known. *Eurypterus remipes* had the spiny chelicerae and walking legs, distinctive broad paddles, and spiked telson that are characteristic of the order. North America and Europe, late Silurian.

Euselachii the sharks and rays, an infraclass of chondrichthyan fish in the subclass Elasmobranchii. For extinct genera see **Selachii** *and* **Batoidea**. Global distribution, Early Devonian to Recent.

Eusthenopteron a genus of large, predatory rhipidistian fish, possibly stem-tetrapods. Fully aquatic, it grew as large as 6 feet long. Differences in its teeth, spine, skull, and especially the bones of its swimming fins may have led to the lobe-finned sarcopterygians and the labyrinthodont amphibians such as *Ichthyostega*. Known from thousands of specimens from Miguasha, Quebec. See also ***Acanthostega*** and **Tetrapoda**. Canada, Middle Devonian, 380 Ma.

Euthacanthus a genus of edentulous acanthodian fish in the family Climatiidae; England and Scotland, Early Devonian.

Eutheria the subclass of mammals that includes all living and extinct placental mammals. The earliest eutherians arose in the Early Cretaceous or perhaps Late Jurassic, and diversified slowly until the beginning of the Paleocene, when they began a very rapid radiation of species into the many ecological niches that became available after the end-Cretaceous extinction. There are 14 orders in the subclass, in some classifications grouped as 4 large clades: Afrotheria, Euarchontoglires, Laurasiatheria, and Xenarthra. Early Cretaceous to Recent.

Euthycarcinoidea an obscure group of arthropods with affinities to both insects and crustaceans. About an inch long, they had a cephalon with small antennae, an abdomen with many legs, and a terminal tail spine. Their fossil record is sparse but widespread: Australia, North America, Scotland, Germany, and France; Silurian to Middle Triassic.

Euthycarcinus "straight crab," a genus of obscure arthropods in the subclass **Euthycarcinoidea**, *q.v.*; known from Germany and France, Carboniferous to Triassic.

Eutriconodonta an order of primitive mammals of the Mesozoic. Formerly called Triconodonta, a polyphyletic grouping, it is now restricted to a monophyletic assemblage of two dozen carnivorous or omnivorous genera. They include several small mammals such as *Yanoconodon*, *Jeholodens*, and *Volaticotherium,* as well as the largest Mesozoic mammals: *Jugulator amplissimus*, somewhat larger than *Volaticotherium*, and the badger-size *Repenomamus* (3 feet long and weighing 30 pounds). Global distribution except Australia, Early Jurassic to Late Cretaceous.

Evolute "unrolled," especially of ammonoids, loosely coiled, with successive whorls barely overlapping earlier ones, so that all whorls are visible.

Evolutionary adaptation the process by which a taxon, in the course of many generations, accommodates itself to its environment, eventually giving rise to new species as a result of the changes it undergoes because of natural selection.

Exogyra a large genus of oysters, marine bivalves in the extant family Gryphaeidae and extinct subfamily Exogyrinae. Characterized by a massive shell and a spirally twisted left valve, it grew to as much as 5 inches. The ornament varied, some species having thick concentric wrinkles and others long, curving radial ribbing. Global distribution but declining after the Cretaceous; Jurassic to Miocene.

Exoskeleton an external shell that protects and supports the body, generally made of chitin or calcium carbonate; a trait of insects, spiders, crustaceans, or shellfish.

Extinction the global disappearance of a taxon resulting from its failure to produce surviving direct descendants. A marked decrease in the amount of life on Earth is referred to as a mass extinction. Background extinctions are those that occur continuously between the periods of mass extinction. The extinctions at the end of the Ordovician, Devonian, Triassic, Permian, and Cretaceous periods are considered mass extinctions, and it is likely that there were other mass extinctions before the Phanerozoic.

F

Fabaceae the principal family of plants in the order Fabales. The most prominent subfamilies are the Papilionoideae and Mimosoideae, important for their role in fixing atmospheric nitrogen in concert with symbiotic bacteria such as the Rhizobiales. The earliest-known fossil specimens have been found in Paleocene strata, but the family's roots go back to the radiation of angiosperms in the Early Cretaceous. Global distribution, Paleocene to Recent.

Facultative having the ability to optionally perform alternative biological functions, commonly used in reference to marine organisms that may either move about in the environment or remain in one place; see also **obligate**.

Falcarius utahensis a species of primitive therizinosaurid theropod dinosaurs, known only from the Cedar Mountain Formation of Utah. About 13 feet long and 4 feet tall, it is named for its large, sickle-shaped claws. *Falcarius* is notable for its herbivorous characteristics—small teeth adapted for shredding leaves, large gut, stout legs, and a long neck—all of which contrast with its smaller and faster carnivorous ancestors and seem to connect *Falcarius* with the later therizinosaurs, which were large herbivores. Early Cretaceous, 126 Ma.

Falcatus a genus of very small early sharks, notable for an unusual dorsal fin that hung over the head of the male. It also had a tall and strongly forked tail and very small pectoral and pelvic fins. United States, Carboniferous (Middle Mississippian to Early Pennsylvanian).

Falls of the Ohio Fossil Beds an exposure of limestone in the Ohio River that contains a great variety of marine invertebrate fossils, especially rugose and tabulate corals. United States, Early to Middle Devonian.

Fasciolariidae a large and diverse family of carnivorous marine snails in the superfamily Buccinoidea. Commonly called spindle snails for their shape, the family

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includes most of the snails formerly named *Fusus*. Ranging up to 2 feet in length, most are 2–4 inches long. They are generally long and high-spired, and many are extremely slender; the aperture is long and open. Global distribution, Cretaceous to Recent.

Faunal assemblage a grouping of associated animal fossils found in a particular stratum.

Faunal succession the principle that groups of fauna and flora change over time, each succeeding group above the previous group in sedimentary rock strata that are often characteristic of certain intervals of time. Established early in the nineteenth century by William Smith, it is the basic concept of biostratigraphy.

Faunal zone a period of time or a stratigraphic unit that is characterized by the presence of a unique assemblage of fossils known as a guide fauna.

Faunule a small fauna, especially a small group of animal fossils found only in a single stratum.

Favositidae a large family of colonial corals in the order Tabulata. The small and tightly packed corallites are long, thin tubes with punctate walls pierced by mural pores. The type genus *Favosites*, called honeycomb coral, is especially important in petroleum geology. See also **Vaughaniidae**. Global distribution, Late Ordovician to Late Triassic.

Faxinalipterus minima a species of small diapsids, poorly known but possibly an early pterosaur. Sparrow-sized, it is known only from fragmentary jaw and limb remains. Brazil, Late Triassic, 220–215 Ma.

Fayum Depression a large basin about 200 miles southwest of Cairo, Egypt. It is important especially for the fossils of primates such as *Aegyptopithecus*, *Catopithecus*, *Karanisia*, *Plesiopithecus*, *Saharagalago*, and the Parapithecidae. Late Eocene to middle Oligocene.

Felidae a family of carnivorous mammals in the order Carnivora and superfamily Aeluroidea. The modern felids include lions, tigers, jaguars, leopards, cheetahs, and the other smaller cats.

Although the line of descent is unclear, their carnivore ancestors include the Miacidae and possibly the Viverravidae; they are generally thought to have evolved from the Miacidae at the end of Eocene.

Fenestella a very large genus of stenolaemate bryozoans in the family Fenestellidae. Its fan-shaped colonies with a netlike surface were especially widespread from the Middle Devonian to the late Permian. Global distribution, Middle Ordovician to Late Triassic.

Fenestellidae a large family of stenolaemate bryozoans in the order Fenestrida. The colony's skeleton consists of many stiff, bifurcating branches connected by crossing arms, resulting in a fenestrate, fan-shaped net. The shape, position, and orientation of the zooecia, used to identify different species, vary greatly. Global distribution, Ordovician to Late Triassic.

Fenestra in biology, a small opening in an organism's body. In paleontology, fenestrae are important usually as slits or holes in the skull, often behind the orbits (as in diapsids and synapsids), or in an individual plate or bone (as in a neck frill). The root *fenestr-* also appears in many names of organisms with netlike structures, especially bryozoans.

Fenestraspis a monospecific genus of phacopid trilobites in the family Dalmanitidae. *Fenestraspis amauta* is characterized by posterior fenestrae of unknown functionality, upwardly directed spines on the entire body, and eye stalks an inch high with a palpebral lobe at the top. Bolivia, Early Devonian, 408 Ma.

Fenestrata an order of stenolaemate bryozoans that includes several suborders, generally characterized by netlike structures; global distribution, Ordovician to Paleocene.

Fenestrida an order of stenolaemate bryozoans that includes the well-known family Fenestellidae and the Early to Middle Devonian Semicosciniidae.

Fenxiang biota a collection of Early Ordovician organisms found in the Fenxiang Formation of Hubei Province, Southern China. Depositional circumstances allowed exceptional preservation of soft tissue, including in brachiopods, antipatharians, and other so far unidentified organisms. See also **Antipatharia**. China, 477 Ma.

Ferecetotherium see **Physeteridae**.

Fermeuse Formation one of several formations on the Avalon Peninsula in Newfoundland containing fossils of the Ediacaran **Mistaken Point** assemblage, *q.v.*

Fezouata Formation a Tremadocian Konservat-Lagerstatten in Morocco, discovered in the 1990s, that has produced very well-preserved fossils from a period between the Lagerstätten of the Cambrian and the Soom Shale of the Late Ordovician. The benthic composition of the Fezouata biota is surprisingly similar to that of the Burgess Shale and Chengjiang biotas, including anomalocaridids and possible naraoiids. Among the newly described species are the sponge *Pirania auraeum* and a possible marrellomorph from Fezouata, tentatively named *Furca mauretanica*. North Africa, Early Ordovician, 480–477 Ma.

Filicopsida the ferns, a class of plants in the division Tracheophyta, formerly called Pteridophyta and Polypodiopsida. The origins and the classification of ferns are unclear. Global distribution, Devonian to Recent.

First Family Site the location in Hadar, Ethiopia, of a cluster of finds of *Australopithecus afarensis*, including some nearly complete skeletons, the most famous called "Lucy." Most of these specimens are dated between 3.2 and 3.4 Ma.

Fistuliporidae a large and diverse family of stemless marine bryozoans in the class Stenolaemata and extinct order Cystoporata. The colonies were initially encrusting, and later genera became dendroid. Global distribution, Silurian to Late Triassic.

Flatfish fish with the unusual pleuronectiform character of having both eyes on the top side of the body. This trait has made flatfish important in the history of evolution and research on some transitional species showing gradual movement of one eye toward the upper side. See ***Amphistium***, ***Gerrothorax***, and ***Heteronectes*.**

Flatworm see **Platyhelminthes**.

Flexibilia a small subclass of stalked or creeping crinoids,

characterized by a flexible tegmen with open ambulacral grooves, the calycal plates being loosely united. Global distribution, Middle Ordovician to late Permian.

Flinders Ranges a site in South Australia where many Precambrian fossils have been found in the Ediacara Hills, especially in the Nilpena site of the Ediacara Conservation Park.

Florissant Fossil Beds National Monument an important site in Central Colorado for insects and plants in lacustrine deposits of volcanic ash laid down at the boundary of the Eocene and Oligocene. It contains large petrified stumps of sequoia-like trees, well-preserved insects, and many angiosperms. North America, late Eocene.

Florissantia a genus of sterculioid angiosperms in the family Malvaceae. Its 1-inch-wide five-petaled flowers have been found throughout North America, especially in Oregon and the Florissant Fossil Beds of Colorado. North America, Eocene to Oligocene.

Flysch see **Aberystwyth**.

Fohsella Formerly known as *Globorotalia*, *Fohsella* is a famous genus of planktic foraminifera in the family Globorotaliidae. *Fohsella* has traditionally been considered a prime example of gradual phyletic evolution, although this status has been challenged by several microstudies since 2006. Cosmopolitan, middle Miocene.

Fontechevade Man name given to two hominin specimens found at Fontechevade, France. Bearing characteristics of both *H. sapiens* and *H. neanderthalensis*, they were first dated as Pliocene and interpreted as an early appearance of modern humans in Europe, antedating Neanderthals. But research in 2007 dated them as Pleistocene, when *H. sapiens* and *H. neanderthalensis* coexisted.

Foraminifera a class of one-celled organisms in the phylum Retaria, almost all aquatic and mostly marine. They are usually less than 2 mm but range up to several centimeters long. These one-celled organisms are mostly benthic, living on or under the sea floor, while a few are planktic. Most foraminiferans develop a calcitic test, often in several concentric layers, so that many are important index fossils. Planispiral taxa are coiled in either an evolute or an involute manner. Almost 9,000 extant and almost 2,000 extinct species are known. Cambrian to Recent.

Fordilla the earliest-known bivalve, a widespread genus of small, primitive bivalves in the order Fordillida. Suboval and about one-tenth of an inch long, only three species of *Fordilla* are currently recognized, all from the early Cambrian, about 520 Ma. See also ***Pojetaia***.

Formicidae the ants, a family of hymenopteran insects in the superfamily Vespoidea. Ants evolved from primitive wasps between 130 and 100 Ma, along with the flowering plants. They became the ecologically dominant insect worldwide by the end of the Paleocene, and 10% of the species known from the Eocene are still present. Early Cretaceous to Recent.

Form taxon a traditional biological classification of a part of an organism, used when the relationship of the part to the whole organism is unclear, and mainly for plants because they seldom fossilize whole; also referred to as a parataxon. See also ***Lyginopteris***.

Form taxonomy a taxonomic system based primarily on morphology rather than on phylogeny (biological relationship).

Fort Union Formation a formation in the Powder River Valley in Wyoming and Montana that straddles the period between the end of the Cretaceous and the beginning of the Paleocene. It contains many important fossils, such as a still-unnamed ornithurine bird that may have survived the extinction, the taeniodont mammal *Alveugena*, and plant fossils such as *Cercidiphyllum*. 66–64 Ma.

Fossil There are two primary types of fossils. Body fossils are parts of an organism preserved by carbonization or permineralization or as casts or molds. Trace fossils, such as worm and mammal tunnels or tracks, are records of some action of an organism. Fossils are typically found in sedimentary strata but may be found deformed in metamorphic deposits. Mud flows and lahars also often preserve many types of fossils and occasionally so do even igneous lava flows.

Fossiliferous fossil-bearing, referring to any deposit or stratum of rock that contains the fossilized remains of an organism.

Fossil record quality The fossil record is inherently incomplete for many reasons. For instance, the nature of marine and lacustrine deposits inevitably results in a more complete and clearer set of specimens than from terrestrial deposits. For specific problems, see **ghost lineage, Lazarus taxon, aragonite,** and **dimorphic.**

Fossorial adapted to digging and living in burrows, typical of many rodents but also badgers and some bees and wasps.

Fossoriality the habit of living in burrows underground, known in many instances since the Paleozoic but increasingly important as a lifestyle for small animals as open grassland increased globally during the Miocene.

Fractofusus misrai an Ediacaran rangeomorph fossil known only from the Mistaken Point assemblage; Newfoundland, Canada, 575–560 Ma**.**

Frondicularia a genus of generally leaf-shaped foraminifera in the family Lagenidae; global distribution, Triassic to Recent.

Fruitadens haagarorum a species of small herbivorous ornithischian dinosaurs in the family Heterodontosauridae, closely related to horned, duck-billed, and armored dinosaurs. Known only from a site in Fruita, Colorado, it is the smallest known ornithischian: about 4 inches high, between 2 and 3 feet long, and weighing less than 2 pounds. Like modern birds, it ate primarily fruit and insects. United States, Late Jurassic, 150 Ma.

Fruitafossor a monospecific genus of small burrowing mammals, probably representing a separate basal mammalian lineage. Known only from one almost complete skeleton found near Fruita, Colorado, in 2005, *F. windscheffeli* was only 4 inches long but had several adaptations for fossoriality and probably fed mainly on termites. It has an unusual set of transitional features indicating that it is close to the roots of modern mammals. It is a striking example of convergent evolution, being unrelated to anteaters or any other known animals with similar habits. United States, Late Jurassic, 150 Ma.

Fullerenes the term for a molecule of carbon in a hollow sphere or other shape. They form closed carbon lattices found in rocks, and because they may trap atmospheric gases at the time the rocks are formed, they have been used since the 1990s to investigate atmospheric changes in different geological time periods. For example, some investigators claim that fullerenes from some end-Permian rocks display noble-gas isotope ratios that are typical of meteorites**,** not Earth; these ratios are possibly evidence of a meteorite impact that may have contributed to the end-Permian extinction.

Funisia dorothea an obscure species of Precambrian segmented worms. Known only from Australian sites dated near the end of the Ediacaran, it was tubular, about a foot long, grew colonially, and may have reproduced sexually. South Australia, 570–540 Ma.

Furcula generally, the wishbone of birds and some dinosaurs, but see also **Collembola**.

Fusiform spindle-shaped, tapered at each end.

Fusulinida an extinct order of foraminiferans, important as index fossils between the Devonian and the end of the Permian. The order contains three superfamilies — the Endothyroidea, Fusulinoidea, and Parathuramminoidea. Global distribution, early Silurian to late Permian.

Fusulinidae a family of large, spindle-shaped foraminiferans in the superfamily Fusulinoidea. Fusulinids are mostly about the size of a grain of wheat, but some are as long as 2 inches. Global distribution, Early Pennsylvanian to late Permian.

Fusulinoidea a superfamily of foraminiferans in the extinct order Fusulinida. It comprises the families Fusulinidae, Ozawainellidae, Schwagerinidae, Staffellidae, and Verbeekinidae. Global distribution, generally considered extinct at the end of the Permian.

Futalognkosaurus a genus of herbivorous sauropod dinosaurs. Known from three partial specimens, it was found near Lake Barreales in Argentina in 2000. One of the largest dinosaurs known, it is estimated to have been at least 90 feet long. Late Cretaceous, 88–86 Ma.

Fuxianhuia protensa a controversial species of early Cambrian basal arthropods. Known from several specimens, it was about 2 inches long, with a sclerite-covered head and segmented thorax and narrow abdomen. Its possible relationship to the coeval *Chengjiangocaris* and maybe even *Canadaspis* is disputed. Chengjiang biota, China, 520–516 Ma.

G

Galeaspida a class or subclass of jawless fish, similar in shape to the heterostracans but more closely related to the osteostracans. They are notable for a flattened, one-piece bony headshield, with an opening of various shapes and sizes on the headshield. Some bore striking slender processes projecting laterally or forward. China and Vietnam, early Silurian to Early Devonian.

Galeopithecidae an extant family of euarchontan mammals in the order Dermoptera. Africa and Southeast Asia, late Miocene to Recent.

Galeritidae a family of irregular echinoids in the superfamily Conulidea. Characterized by simple plating and a thick shell, they have a relatively smooth surface and a subconical shape. They appeared about 70 Ma and became extinct at the end of the Cretaceous. Europe and Asia.

Galliformes the order of birds that includes chickens, pheasants, turkeys, guinea fowl, and grouse. The galliforms probably arose in the late Cretaceous, but few Cretaceous candidates have been proposed; one is *Vegavis iaai*, a possible anseriform bird found in Antarctica. Several galliform families had appeared by the Eocene – the Numididae, Phasianidae, and probably the Megapodiidae. Global distribution, Cretaceous to Recent.

Gampsonychidae a family of primitive crustaceans in the extinct order Palaeocaridacea, possibly related to the eurypterids; Carboniferous.

Ganoid scales fish scales with a bony, enamel-like surface, common in sturgeon and gar. Ganoid scales are generally diamond-shaped and nonoverlapping but are linked together at joints.

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Gansus yumenensis a species of Early Cretaceous birds found in Gansu and Liaoning Provinces. Known from several partial specimens that resemble in various ways, *Hesperornis*, loons, and ducks, it seems to be close to the ancestry of modern birds. Chin, 120 Ma.

Garstang's Hypothesis (of vertebrate origins) an early twentieth-century theory of chordate evolution that proposed an alternative route for chordate evolution from echinoderms. Garstang opposed Ernst Haeckel's theory, based on the principle that ontogeny recapitulates phylogeny, which is now discredited. Most aspects of Garstang's theory are now accepted.

Gasparinisaura cincosaltensis a species of herbivorous ornithopod dinosaurs. About 6 feet long, it weighed about 40 pounds. Argentina, Late Cretaceous, 85–82 Ma.

Gastonia a genus of basal ankylosaurian dinosaurs, tentatively classified in the family Nodosauridae. From 15 to 20 feet long and about 1 ton, *Gastonia* had a strong set of spikes, scutes, and plates. Utah, United States, Early Cretaceous, 126–123 Ma.

Gastornis a genus of large flightless birds in the order Anseriformes. It had a massive skull, heavy bill, and robust legs and was probably a good runner. The largest species, *G. giganteus* and *Diatryma*, grew to almost 7 feet high and were about the size of the largest moas. Although *Gastornis* resembles the carnivorous South American phorusrhacids of the Miocene, the two groups are not related. Researchers still dispute whether they were herbivorous, carnivorous, or both; the massive bill was only slightly hooked and seems to be suited to a herbivorous diet. Canada and Europe, late Paleocene to Eocene.

Gastralia (singular: gastralium): Dermal bones in the ventral body wall of some dinosaurs and many reptiles, especially crocodilians, pelycosaurs, and early turtles. Gastralia provide abdominal support without being connected to the vertebrae.

Gastrioceras a genus of goniatitic ammonoids in the family Gastrioceratidae. It is characterized by a wide umbilicus and a globose shell with a goniatitic (simple and relatively smooth) suture pattern. Widespread in the Middle to Late Pennsylvanian, several species are index fossils. North America and Europe, Late Carboniferous, possibly to Permian.

Gastropoda "stomach foot," the most speciose class of mollusks, including slugs; limpets; and land, marine, and freshwater snails. The phylogeny of the class is highly disputed, but four subclasses are generally accepted: Caenogastropoda, Heterobranchia, Patellogastropoda, and Vetigastropoda. Some classifications include the Neritimorpha as a fifth subclass. For possible early gastropods, see ***Chippewaella*** and ***Strepsodiscus***. See also **Archaeogastropoda** and

Mesogastropoda, abandoned classifications. Global distribution, late Cambrian to Recent.

Gavialoidea the gharials, an extant superfamily of squamate reptiles in the order Crocodylia (which includes the alligators and the crocodiles). Gavialoidea survives only as *Gavialis gangeticus* in northern India and *Tomistoma schlegelii* in scattered locations between Malaysia and Indonesia. Specialized fish eaters, they are more aquatic than the other extant crocodilians, with weak forelimbs and a longer, more powerful tail. Lined with more than 100 interlocking teeth, their long, narrow snout is one of the ancestral features shared with their basal forebears such as *Eosuchus* and more recent relatives *Gryposuchus* and *Aktiogavialis*, all of which also had long, narrow snouts and long tails. Global distribution, Early Cretaceous to Recent.

Geiseltaliellus a genus of lizards in the family Iguanidae. See also ***Palaeopython***. Europe, Eocene to Oligocene.

Gekkota an extant clade of lacertilian squamates whose early fossil representatives are widespread but sparsely known. *Eichstaettisaurus* is a probable stem-gekkotan known from Europe in the Late Jurassic, and the basal *Hoburogekko* and *Gobekko* are known, respectively, from the Early and Late Cretaceous of Mongolia. Global distribution, especially tropical and semitropical, Jurassic to Recent.

Gelocidae a family of hornless ungulate mammals, possibly polyphyletically related to the Pecora. They were among the earliest ruminants but were more advanced than the Hypertragulidae. North America, Europe, Asia, and Africa; Eocene and Miocene.

Geminiraptor suarezarum a species of raptor-like dinosaurs in the family Troodontidae, found in Utah in 2010. Its head was large, as in raptors, but since it is known only from a partial jaw bone, its relationship is uncertain. It is dated between 130 and 125 Ma, almost 50 million years earlier than the numerous North American raptors of the Late Cretaceous. United States, Early Cretaceous.

Gemündina a monospecific genus of rhenanid placoderms in the family Asterosteidae. Its flattened body and very large, winglike pectoral fins gave it a shape similar to that of rays (see **Batoidea**), which evolved 200 million years later in the Triassic. *Gemündina stuertzi* is known from several exceptional specimens from the Hunsrück Lagerstätte, notable for the absence of the characteristic placoderm toothplates. Germany, Early Devonian.

Genal referring to the "cheeks" of a trilobite, on both sides of the glabella.

Genasauria a clade of dinosaurs including all ornithischians except Lesothosaurus. The clade includes two groups, the Neornithischia and the Thyreophora. Early Jurassic to Late Cretaceous.

Generalized of an organism, having few specific adaptations to its ecological niche.

Geniohyus a genus of primitive hyraxes in the extinct family Pliohyracidae and subfamily Geniohyinae. Egypt, known only from the early Oligocene.

Genotype the genetic constitution of an organism.

Geologic Time Scale (simplified for this book's purposes)**: Precambrian Eon**, up to 541 Ma, ending in the Neoproterozoic Era, which consists of the Tonian, Cryogenian, and Ediacaran Periods. **Phanerozoic Eon** (541 Ma to the present), consisting of three eras: **Paleozoic Era**, Cambrian, Ordovician, Silurian, Devonian, Carboniferous (for North America, divided into Mississippian and Pennsylvanian Epochs), and Permian; **Mesozoic Era**, Triassic, Jurassic, and Cretaceous; and **Cenozoic Era**, divided into the Paleogene Period (Paleocene, Eocene, and Oligocene Epochs), Neogene Period (Miocene and Pliocene Epochs), and Quaternary Period (Pleistocene and Holocene Epochs). The Phanerozoic periods are divided into epochs and the epochs into shorter spans called ages. For a more detailed list, see the ICZN's International Chronostratigraphic Chart.

Geomichthys see ***Palaeoniscum***.

Geomyidae the pocket gophers, an extant family of fossorial rodents in the superfamily Geomyoidea. They appeared in the Eocene and have flourished throughout North America since the Oligocene. Restricted to North and Central America, Eocene to Recent.

Georgiacetus a genus of protocetid whales in the suborder Archaeoceti. Its pelvis was not attached to its spine, representing the loss of functional hindlimbs in whales' evolution from terrestrial ancestors. Southeastern United States, middle Eocene, 40–37 Ma.

Geosaurus a genus of marine crocodylomorphs in the clade Thalattosuchia, family Metriorhynchidae, and subfamily Geosaurinae. Up to 10 feet long, it is difficult to classify because of small differences in specimens, but it is probably related to *Dakosaurus*, *Cricosaurus*, and *Rhacheosaurus*. South America and Europe, Late Jurassic to Early Cretaceous.

Gerrothorax a probably monospecific genus of temnospondyl amphibians in the suborder Stereospondyli and family Plagiosauridae. It is known only from riverine and lacustrine environments. About 3 feet long and extremely flattened, *G. pulcherrimus* was pleuronectiform, with both eyes on the top of its broad head. It retained its feathery larval gills, so that it could remain underwater indefinitely, probably lying on the bottom awaiting prey. Europe and Greenland, Middle to Late Triassic.

Ghost lineage a hypothetical early occurrence of a lineage, not known from the fossil record but predicted because of the earlier appearance of a sister group. Because of the haphazard nature of fossilization, there are many possible ghost lineages. One of the most obvious examples is that of the chimpanzee. The only *Pan* (chimpanzee) fossils known are three teeth from Kenya, dated at 550,000 years ago in the middle Pleistocene. But genetic analysis and the fossil record of hominids show that the divergence of human ancestors from the chimpanzee lineage most likely occurred at the end of the Miocene, between 7 and 5 Ma. The chief reason for the absence of *Pan* fossils seems to be their usual habitat, lush tropical forest with myriad scavengers, and a highly acidic soil that quickly dissolves bones. But over the course of 6 million years, earlier species of chimpanzees must have existed, and their ghost lineage can reasonably be inferred.

Ghost Ranch a Konzentrat-Lagerstätte in New Mexico that is known for thousands of specimens of dinosaurs from the end of the Triassic; the best-known discovery was the first *Coelophysis*. United States, Late Triassic, 220–202 Ma.

Gibbons see **Hylobatidae**.

Giganotosaurus one of the largest-known carnivores, a genus of theropod dinosaurs in the family Carcharodontosauridae. Up to 43 feet long and weighing up to 14 tons, *Giganotosaurus* was almost as large as *Spinosaurus*. Known only from a skull, femur, lower jaw, and other fragments, the type species is *G. carolinii***.** Argentina, Late Cretaceous, 99–96 Ma.

Gigantopithecus a genus of hominoid primates in the family Pongidae, known from partial skeletons and teeth of the Pliocene in India and the Pleistocene in China, as recent as 100,000 years ago. The largest-known ape, the primarily herbivorous *Gigantopithecus* stood as high as 10 feet and weighed up to 1200 pounds.

Gigantoproductus a genus of large strophomenate brachiopods in the order Productida and the family Monticuliferidae. Up to 12 inches wide, *G. giganteus* is the largest brachiopod known. Cosmopolitan, Middle Mississippian to Early Pennsylvanian.

Gigantopteridales a diverse group of large trees at the end of the Paleozoic, generally considered an order of seed ferns in the division Pteridospermatophyta. Among the most advanced plants of the Paleozoic, they are possible ancestors of later plant forms, including angiosperms. They had many characteristics of flowering plants but are not known to have flowered themselves; in fact, their mode of reproduction is unclear. They appeared near the end of the Permian and flourished in Asia and North America for 10 million years, briefly surviving the great extinction before disappearing in the Early Triassic.

Gigantoraptor erlianensis a species of theropod dinosaurs in the birdlike family Caenagnathidae. Dated at 85 Ma but possibly younger, it had no teeth but had large claws and probably a large beak. Known from a partial skull and skeleton, it is estimated to have been about 25 feet long and 2 tons in weight. Its eggs are among the many large eggs found in China, 1–2 feet long. Mongolia, Late Cretaceous, about 84 Ma.

Gigatitan a genus of large predatory insects in the order Titanoptera. With a 16 inch wingspan and stout spines on the forelegs, *Gigatitan* is notable for fluting on the wings that could produce stridulation when rubbed by the hind legs, in the manner of modern crickets. Madygen Formation, Kyrgyzstan; Late Triassic, 230–225 Ma.

Gilboa stumps see ***Eospermatopteris***.

Gill

1. an opening or extension of the body surface of an aquatic organism to allow gas exchange or suspension feeding.
2. the ribbed lamellae on the underside of mushrooms, used in spore dispersal.

Gill arches rods of bone or cartilage surrounding the gills; see **Gnathostomata** and **Vertebrata.**

Gillicus arcuatus a species of large fish in the family Ichthyodectidae or Saurodontidae. Up to 7 feet long, *Gillicus* was relatively small for an ichthyodectid, preying on zooplankton and small fish. Known from only a few specimens, it lived in the Western Interior Seaway of North America in the Late Cretaceous. The most famous specimen was found in Kansas, inside a 13 foot *Xiphactinus*, probably having caused the death of the larger fish. United States, Late Cretaceous.

Ginkgoites a form genus of the leaves of the Ginkgoales, with indented but not deeply divided fan-shaped leaves; global distribution in the late Mesozoic.

Ginkgophyta a division of gymnospermous plants that first appeared in the late Permian but is now represented by only one genus, *Ginkgo biloba*, in the order Ginkgoales**.** The ginkgos are known in the fossil record primarily by their distinctive lobed and veined leaves.

Giraffatitan a genus of titanosaurian sauropodomorph dinosaurs in the family Brachiosauridae. Known from partial skeletons found in Tanzania, *Giraffatitan* is closely related to *Brachiosaurus*, with similarly elongated forelimbs and a short tail. It is estimated to have been more than 70 feet long and to have weighed up to 80 tons. Tanzania, Late Jurassic.

Giraffokeryx a genus of artiodactyl mammals in the family Giraffidae, similar in appearance to the modern okapi, but with four ossicones. Russia, Pakistan, and Nepal; Miocene, 14–11 Ma.

Girtyocoelia a genus of Permian calcareous sponges in the subclass Ceractinomorpha. An important reef builder late in the Permian, especially in the economically important Permian reef complex of Texas, it seemed to be extinct in the Early Triassic but then reappeared in the Middle Triassic. Close relatives appear earlier, in Ordovician strata, but it is unclear whether they are *Girtyocoelia* itself. A possible new related species named *Girtyocoeliana* was reported in 2018 as a sphinctozoan sponge. United States, Middle Pennsylvanian to Permian or Triassic.

Girvanopyge a genus of deep-ocean trilobites in the order Asaphida and family Cyclopygidae or Remopleurididae. Characterized by large compound eyes, an unusual cylindrical thorax, and a very broad glabella. Europe, Middle to Late Ordovician.

Glabella the convex axial segment of the cephalon in trilobites, usually bulbous on the anterior end. The major organs lie beneath the glabella, which is covered by a solid cephalic shield, the carapace.

Glabrocingulum a genus of low-spired marine snails in the family Gosseletinidae; United States, Carboniferous.

Glacialisaurus a genus of relatively small massospondylid dinosaurs of Antarctica, one of several sauropodomorphs found in the Hanson Formation. It is known only from fragments of two specimens. Early Jurassic, 190 Ma.

Glaucomys a genus of flying squirrels in the subfamily Sciurinae. Found only on the West Coast of North America, they are small and dark-colored and have a patagium. Middle Pleistocene to Recent.

Glenotremites a genus of articulate crinoids in the order Comatulida. Hemispherical and 3–4 inches wide, its calyx was flattened or slightly concave. It was stemless and free-living but could attach to the substrate with well-developed cirri. Europe, Late Cretaceous, 99–89 Ma.

Gliridae an extant family of sciuromorph rodents in the superfamily Gliroidea, descended from the Ischyromyidae. The family includes the modern dormice. Europe, Asia, and Africa; early Eocene to Recent.

Global Boundary Stratotype Sections and Points Markers selected by the International Commission on Stratigraphy on which the International

Chronostratigraphic Chart is based. The choices are based principally on stratigraphic first appearances of particular fossils, with a few extinctions also noted. The list also includes some markers based on paleomagnetic and climatic data. Sometimes referred to as "golden spikes," they are typically identified physically by a brass marker in a particular location. See, for example, ***Cardioceras, Iapetognathus***, ***Marsupites***, and ***Monograptus***.

Globidens a genus of small mosasaurs known for its rounded teeth, specialized for durophagy — crushing turtles, ammonoids, and other hard-shelled animals. North America, Africa, and Asia; Late Cretaceous, 85–66 Ma.

Globigerinida an extant order of globose planktic foraminiferans, important as an index fossil in the Cretaceous. Simple but multi-chambered foramiferans, the globigerines seem to be unusually resistant to mass extinctions. The genus *Globigerina*, which appeared in the Eocene, now dominates, and large areas of ocean floor worldwide are covered by the bodies of various species in the order, constituting what is called a *Globigerina* ooze. In reference to the end-Cretaceous extinction, see also ***Guembelitria***. Global distribution, Jurassic to Recent.

Globorotalia see ***Fohsella***.

Glossopleura a genus of trilobites in the order Corynexochida and family Dolichometopidae. Relatively large, it was 4–5 inches long, with a flattened body, strong genal spines, eight thoracic segments, and a short telson. North America, middle Cambrian, 513–499 Ma.

Glossopterid flora an important group of pteridospermatophyte plants found in Permian and Early Triassic strata laid down in Gondwana. The absence of glossopterids in northern land masses was important early evidence of the existence of the southern supercontinent. Antarctica, Australia, New Zealand, Southern Africa, India, and South America.

Glossopteris a genus of seed ferns in the division Pteridospermatophyta and order Glossopteridales. Characterized by a tongue-shaped leaf with a prominent midrib and veins, arranged spirally around the ends of the branches, it was a dominant plant in the Permian Glossopteris flora of Gondwana but has not been found anywhere in the Northern Hemisphere. It is rare in Triassic and Jurassic deposits. Australia, Antarctica, India, Asia, Southern Africa, and South America; early Permian to Jurassic.

Glyphocyphidae a family of epifaunal sea urchins, irregular echinoids in the extant superorder Echinacea and order Camarodonta. South America, Africa, Europe, and Asia; Early Cretaceous to Eocene.

Glyptagnostus reticulatus a species of trilobites in the family Agnostidae. Isopygous and blind, it is the index fossil for the beginning of the Furongian Series of the Cambrian. Global distribution, late Cambrian, 497 Ma.

Glyptocrinina a suborder of camerate crinoids in the large order Monobathrida. Some glyptocrinids have large, 1 inch thecae. The suborder contains the families Glyptocrinidae and Patelliocrinidae. Middle Ordovician to Early Devonian.

Glyptocrinus a genus of camerate crinoids in the order Monobathrida and family Glyptocrinidae. Very similar to the Late Ordovician *Pycnocrinus*, it had a small, conical cup about 1 inch high, with a striking star-shaped network of ridges on its surface and many slender, branching arms extending up from the cup. The stem is circular, with alternating thick and thin plates. North America, Middle Ordovician to early Silurian.

Glyptodontinae a subfamily of large, heavily armored xenarthran mammals in the extant order Cingulata and family Chlamyphoridae. Their striking armor consisted of a dome-shaped covering of scutes over the whole body and skull. The type genus, *Glyptodon*, was about 11 feet long and almost 5 feet high and weighed up to 2 tons; the southern genus *Doedicurus* was slightly larger. Living in South America for 20 million years, they entered North America in the Pliocene by migrating across the newly formed Panama land bridge. They were probably hunted to extinction by the first humans to arrive in the Americas. South and North America, early Miocene to Pleistocene.

Glyptops a genus of Mesozoic cryptodiran turtles in the family Pleurosternidae. The carapace of the type species, *G. plicatulus*, is about a foot long and is well-represented in the Morrison Formation. United States and possibly China, Late Jurassic to late Cretaceous.

Glyptostrobus an extant genus of trees in the family Cupressaceae. Growing as high as 115 feet, *Glyptostrobus*, related to the modern bald cypress, is still represented by the Chinese swamp cypress, bearing a cone at the tip of a branch covered with scalelike leaves. Extant in Southeast Asia, formerly widespread in North America, Europe, and Asia; Cretaceous to Recent.

Gnathichnus an ichnogenus of trace fossils, star-shaped excavations in carbonate substrates, incised by grazing regular echinoids; Jurassic to Recent.

Gnathobelodon a genus of proboscideans in the family Gomphotheriidae, notable for a projecting jawbone that resembled a shoehorn. It was similar to *Amebelodon* and *Platybelodon* except for having no lower tusks but simply the long jawbone. United States, middle to late Miocene.

Gnathodontidae a family of conodonts in the order Ozarkodinida. Widespread in the early Carboniferous, they declined rapidly and became extinct in the early Permian.

Gnathostomata (echinoids): a superorder of irregular sea urchins that possess a feeding lantern; lower Jurassic to Recent.

Gnathostomata (vertebrates): "jaw-mouthed," a superclass or infraphylum of jawed vertebrates. The gnathostomes appeared in the Middle Ordovician, derived from agnathans that had developed pectoral and pelvic fins as well as enlarged anterior gill arches, which folded over forward in some species, gradually becoming upper and lower jaws. Jaws gave such an advantage in predation that the gnathostomes became the dominant vertebrates in the oceans from the Silurian through the Early Devonian. By the end of the Devonian, almost all agnathans had become extinct. The gnathostomes were the ancestors of almost all modern vertebrates, descending through placoderms or osteichthyans. See also ***Entelognathus***. Middle Ordovician to Recent.

Gnetales an extant order of gymnosperm plants in the class Gnetophyta. The Gnetales have an unusual vascular system similar to that of angiosperms and have been suggested as possible ancestors of the flowering plants. The three extant genera include *Welwitschia*, *Gnetum*, and *Ephedra*. Global distribution, Permian to Recent.

GOBE the Great Ordovician Biodiversification Event; see **Ordovician**.

Gobiatherium a genus of herbivorous dinoceratan mammals in the mainly North American family Uintatheriidae, sometimes placed in its own subfamily, Gobiatheriinae. It was about 10 feet long, and its low skull bore none of the horns, tusks, or knobs characteristic of its North American relatives. Mongolia, middle to late Eocene.

Gobipteryx a genus of early toothless enantiornithean birds. Until 1995, when *Confuciusornis* was discovered, *Gobipteryx* was the earliest-known beaked bird. Mongolia, Late Cretaceous, 75–70 Ma.

Gogia a genus of echinoderms in the paraphyletic class Eocrinoidea and family Eocrinidae. A common middle Cambrian eocrinoid, the plate-covered *Gogia* was one of the earliest stalked echinoderms, dating back to the late early Cambrian and disappearing toward the end of the period. North America and Spain.

Gogo Formation an Upper Devonian (Frasnian) site in Western Australia, a Konservat-Lagerstatten containing exceptionally well-preserved soft-tissue fossils. Among its notable specimens are three species of armored placoderm fish that seem to have been viviparous: *Austroptyctodus gardineri, Materpiscis attenboroughi,* and

Incisoscutum ritchiei. Specimens of these species show evidence of fertilization of eggs inside a female fish occurring as much as 30 million years earlier than previously thought, around 380 Ma. Since the fish evidently gave birth to live young, the two fossils represent the earliest-known vertebrate mothers. The specimen of *Materpiscis* contains a fetus and an umbilical cord.

Golden spike term referring to a specific location where a first or last occurrence of an index fossil can be found.

Gomphos elkema the oldest complete skeleton of a rabbitlike mammal, found in the Nemegt Basin of Mongolia**.** Closely related to both lagomorphs and rodents, it supports the idea that the two groups shared a common ancestor that lived near the end of the Cretaceous. It also indicates that lagomorphs appeared no earlier than 65 Ma. Mongolia, 55–50 Ma.

Gomphotheriidae a diverse family of proboscideans in the suborder Gomphotherioidea. The largest species weighed up to 7 tons and were about 10 feet high at the shoulder; most species had four tusks and may have had elephant-like trunks. The last of the gomphotheres became extinct about 9,000 years ago. Global distribution except Australia, late Oligocene to Holocene.

Gomphotherium a genus of proboscideans in the family Gomphotheriidae. Almost 8 feet high at the shoulder and weighing 5 tons, it had four tusks. North America, Europe, Asia, and Africa; early Miocene to early Pleistocene.

Gondwana the Paleozoic southern supercontinent, named for the Gondwana geological system (dated from the Carboniferous to the Jurassic) in the region of India where early *Glossopteris* investigations occurred. Located in the lower part of the Southern Hemisphere, Gondwana included what is now South America, Africa, Madagascar, India, Antarctica, Australia, New Zealand, and the related islands of Australasia. In the late Paleozoic, Gondwana was the southern part of the global supercontinent Pangaea. Modern faunas in this Austral realm continue to be markedly different from more northern faunas. For dates see **paleogeography**.

Gondwanascorpio emzantsiensis a species of chelicerates in the class Arachnida and order Scorpiones. One of the oldest true scorpions, it is known from a pincer and sting found in a South African stratum that was much nearer the South Pole in the Famennian. See also ***Brontoscorpio***. South Africa, Late Devonian, 360 Ma.

Gondwanatheria a group of primitive mammals known mainly from fragmentary specimens in the Southern Hemisphere, probably related to haramiyidans and multituberculates. A discovery in 2010 of *Vintana sertichi*, an almost complete skull of a 20 pound gondwanatherian, greatly expanded knowledge of the group. See also ***Cifelliodon***. Argentina, Madagascar, and Antarctica; Late Cretaceous to Miocene.

Goniatitida a large order of Paleozoic ammonoids, descended from the Agoniatitida. They were planispiral and relatively small, mostly from 2 to 6 inches high. Their goniatitic sutures formed a simple pattern of smooth lobes and saddles. Widespread from the Devonian to the end of the Permian.

Goniopholis a genus of medium-sized crocodylomorphs in the clade Thalattosuchia and family Goniopholididae. From 6 to 9 feet long, *Goniopholis* was very similar to modern crocodiles and is considered a neosuchian. Possibly the earliest goniopholidid is *Calsoyasuchus*, known from a partial skull found in Arizona and dated at 196.5 Ma. Cosmopolitan, Late Jurassic to Early Cretaceous.

Goniophora a genus of Paleozoic marine bivalves in the order Modiomorphida and family Modiomorphidae. Between 3 and 4 inches long, *Goniophora* had an unusually lopsided shape, with sharp beaks and a ridge line extending the length of both valves. Global distribution, Early Ordovician to late Permian.

Goniopora an extant genus of colonial scleractinian corals in the family Poritidae. *Goniopora* is generally massive, but some species were branching. Global distribution, Early Cretaceous to Recent.

Gonolkites see ***Parkinsonia***.

Gorgonopsidae a family of theriodont therapsids. Early gorgonopsians were dog-sized, and some later species were the size of a large bear. They had a heterodont dentition and other mammalian characters but are not considered in the direct line of descent to mammals, which goes through their cousins the cynodonts. The family essentially disappeared in the Permian extinction, but see ***Cyonosaurus***. Southern Africa and Russia, middle to late Permian.

Gorgosaurus a genus of tyrannosaurid dinosaurs in the subfamily Albertosaurinae. Bipedal, as long as 30 feet and weighing almost 3 tons, it was smaller than its cousins *Tyrannosaurus* and *Tarbosaurus*. A striking *Gorgosaurus* exhibit at the Royal Tyrrell Museum displays a reconstructed skeleton containing the original bones alongside a replica wall showing the actual discovery position of the bones. Canada, Late Cretaceous, 77–75 Ma.

Gracilisaurus see **Weigeltisauridae**.

Gradualism see **phyletic gradualism** and **uniformitarianism.**

Graeophonus an extant genus of "whip spiders," chelicerate arachnids in the order Amblypygi or Paleoamblypygi. About half an inch long, three species of *Graeophonus* are known from Carboniferous sites in Nova Scotia, Illinois, and England. Global distribution, Carboniferous to Recent.

Gramineae see **Poaceae**.

Grammysia a genus of small marine bivalves in the order Cardiidia and family Grammysiidae. It has a suboval outline and is characterized by a blunt, incurved beak and a deep, oblique fold across the middle of the shell. Global distribution, Middle Ordovician to Early Carboniferous.

Grande Coupure a term used for the great turnover of mammalian faunas in Europe at the boundary of the Eocene and Oligocene, marked especially by the migration into Europe of many new Asian taxa.

Graptolithina "rock writing," the graptolites, a class of colonial marine invertebrates in the subphylum Hemichordata, probably related to the extant pterobranchs. A graptolite colony is called a rhabdosome and has a varying number of rodlike stipes (branches); the individual zooids were housed in thecae on the stipes. Very little is known about the structure, morphology, or feeding habits of the zooids (see **Psigraptus**). The largest zooids were about an 8 inch long, and they probably could not leave the theca. Graptolites evolved from bottom-encrusting to sessile forms in the Cambrian, with the earliest sessile order, the Dendroidea, persisting to the Carboniferous. It gave rise to the planktic Graptoloidea, which diversified rapidly worldwide during the Ordovician.

Graptolites are important as index fossils of the early and middle Paleozoic Era because of their global occurrence and their rapid evolution and radiation into many different species. The strata of the Ordovician and Silurian have been divided into graptolite biozones of about one million years each. The anisograptid, dichograptid, diplograptid, leptograptid, and monograptid faunas are the most important. See also ***Chaunograptus***. Middle Cambrian to Carboniferous, global distribution in the Ordovician and Silurian.

Graptoloidea an order of graptolites and the only completely planktic group. Generally with a smaller number of stipes than the Dendroidea, they appeared early in the Ordovician and became the most prominent planktic animals worldwide until their extinction in the Devonian. Early Ordovician to Early Devonian.

Grasses see **Poaceae.**

Great American Biotic Interchange the mingling of animal populations between South and North America that was made possible by the rise of the Isthmus of Panama, generally thought to have occurred between 7 and 3 Ma but possibly begun as much as 10 million years earlier. The two continents had been separate since the early Paleocene, and only a few terrestrial animals had moved from one continent to the other until the late Pliocene (such as the island-hopping *Cyonasua* in the late Miocene). The interchange resulted in many regional changes, notably the extinction of several South American groups because of the introduction of large new predators from the north.

Great Oolite name given to a group of Middle Jurassic formations known mainly from the region of Bath, England. The Great Oolite consists principally of oolitic and other types of limestone. It is dated in the Bathonian, between the Bajocian and Callovian, and is especially important for several species of dinosaurs. Its zones are dated by species of ammonoids such as *Parkinsonia* and *Tulites*. Underlying it is the Inferior Oolite, a formation of similar composition that contains fossils from the Aalenian and Bajocian. The Great Oolite produces a prized building stone used especially around Bath, and the Inferior Oolite is characteristic of buildings in Dorset, to the southeast. England, 174–166.

Great Oxygenation Event term referring to the production of oxygen by organisms, mainly cyanobacteria, in the Paleoproterozoic Era. Although the timing and causes are widely debated, significant oxygen production began around 2,400 Ma and resulted in levels of atmospheric oxygen sufficient for complex oxygen-breathing and sexually reproducing organisms sometime in the Neoproterozoic Era, between 1000 and 600 Ma.

Green River Formation a mainly Eocene formation with significant outcroppings in Colorado, Utah, and Wyoming, including at Dinosaur and Fossil Butte National Monuments. The formation has produced large numbers of fish in finely varved lacustrine strata, so that it can be considered both a Konzentrat- and a Konservat-Lagerstatten. Other important fossils are early bats, a complete skeleton of *Hyracotherium*, the North American crocodilian *Borealosuchus*, the freshwater stingray *Heliobatis*, the soft-shell turtle *Trionyx*, and many other turtles, snakes, plants, and insects. United States, late Paleocene to late Eocene, 56–49 Ma.

Greererpeton burkemorani a genus of stem-tetrapod amphibians in the family Colosteidae, dated at about 340 Ma. Almost 5 feet long, its body was eellike, with a flattened skull 7 inches long. The short limbs had five digits but were used mainly for steering in the water. It was almost completely aquatic, remaining in rivers and lakes, while other stem-tetrapods were moving ashore in the Carboniferous. North America, Late Mississippian.

Grès à Voltzia a Middle Triassic Konservat-Lagerstatten in Northeastern France, dated about 243 Ma. Its brackish-water deposits were laid down in a deltaic environment similar to that of the Carboniferous Mazon Creek site. The finely laminated clay rock of the Grès à Meules stratum contains very well-preserved specimens of terrestrial and aquatic fossils, including plants, millipedes and other arthropods, brachiopods, crustaceans, and insects. Fish (see ***Dipteronotus***) and amphibians, mainly capitosaurid temnospondyls, are also represented.

Griffithides see ***Phillipsia***.

Grippidia see ***Chaohusaurus***.

Groeberiidae a small family of South American marsupials. They were rodent-like, but in skull architecture and dentition, they differed from all other mammals. Argentina and Chile, late Eocene to early Oligocene.

Groenlandaspis a genus of arthrodire placoderm fish. Ranging from 3 to 19 inches long, it had small toothplates and strong, pyramid-shaped thoracic armor. Global distribution, Late Devonian.

Gryphaea a genus of bivalves in the order Ostreoida and family Gryphaeidae. From 3 to 4 inches long, the distinctively convoluted *Gryphaea* is characterized by prominent growth bands in the thick, coiling upper valve; the lower valve is much smaller, flat, and lid-like. It was considered in the first half of the twentieth century to be a possible example of orthogenesis because of an erroneous interpretation of its coiling growth pattern, disproved by Anthony Hallam and Stephen Gould. Global distribution, Late Triassic to Eocene.

Gryphaeidae an extant family of bivalves, sometimes called "foam oysters," in the order Ostreoida; global distribution, Middle Triassic to Recent.

Gryposaurus a genus of hadrosaurid dinosaurs in the subfamily Saurolophinae, similar to *Kritosaurus*. A duckbill with a high nasal arch on its long skull, *Gryposaurus* was about 30 feet long. It probably ate many kinds of vegetation, having as many as 800 teeth, up to an inch long and set in a powerful jaw. Its three species are known from locations near the Western Interior Seaway in Alberta, Montana, and Utah. North America, Late Cretaceous, 83–74 Ma.

Gryposuchus a South American genus of large gharials in the superfamily Gavialoidea. It grew to as long as 30 feet and had the narrow snout and relatively long tail of the modern gharials. South America, middle Miocene to Pleistocene.

GSSP see **Global Boundary Stratotype**.

Guaibasaurida*e* an early family of sauropodomorph dinosaurs. First proposed in 1999, its makeup is still in flux; see ***Panphagia*****,** ***Chromogisaurus*****,** ***Agnosphitys*****,** and **Saurischia**. Argentina and Brazil, Late Triassic, 231–208 Ma.

Gualicho shinyae a species of allosaurid theropod dinosaurs similar but not closely related to *Tyrannosaurus rex* and also described as similar to *Deltadromeus* but with much shorter forelimbs. Known from a partial skeleton found in the Huincul Formation of Argentina and described in 2016, it was about 16 feet long and weighed half a ton. Like *T. rex*, *Gualicho* had a two-digit manus on forelimbs the size of those of a human child, a result of convergent evolution. Argentina, Late Cretaceous, 95 Ma.

Guanlong wucaii a species of theropod dinosaurs in the superfamily Tyrannosauroidea, perhaps the earliest basal tyrannosauroid. Bipedal and known from two partial skeletons, *Guanlong* was only about 4 feet high and 10 feet long, with three digits on its strong forelimbs. It bore a large but fragile crest on its forehead, stretching from behind the nostrils to just behind the eyes and about 3 inches high. The function of the crest is not known, but it would appear to be a liability in combat, since it is only as thick as a tortilla. Western China, Late Jurassic, 160 Ma.

Guanshan biota a fauna of exceptionally preserved fossils found in eastern Yunnan, China, near the site of the better-known Chengjiang biota. The estimated date of the Guanshan biota (ca. 512 Ma) lies between that of the Burgess Shale (508 Ma) and the Chengjiang biota (ca. 515 Ma), and the three faunas are remarkably similar. China, early Cambrian, 515–510 Ma.

Guembelitria cretacea a species of planktic foraminiferans in the order Globigerinida and family Guembelitriidae. Known as an opportunistic disaster species because, although rare at the end of the Cretaceous, it is the most common of several foraminiferans that survived into the Paleocene. Abundant in the earliest Paleocene strata, it evidently thrived in the environmental conditions following the extinction of many other species. See also **Globigerinida**. Europe, Australia, Asia, and South America; Cretaceous to Oligocene.

Gueragama a genus of acrodont squamates in the suborder Iguania. Significantly, it is the only acrodont lizard known from South America, supporting the belief that acrodontans once spread across Gondwana before being replaced by non-acrodontans in the Americas. Brazil, Late Cretaceous, 88–85 Ma.

Guide fossil see **index fossil.**

Guildayichthys a genus of early marine actinopterygian fish in the order Guildayichthyiformes. Only about 2 inches long, it had short, conical teeth. Its disc-shaped body and robust pectoral, dorsal, and anal fins gave it good maneuverability. See also ***Discoserra***. United States, Early Carboniferous.

Guiyu oneiros a species of sarcopterygian fish, the earliest-known articulated specimen of an osteichthyan. About a foot long, with ganoid scales, it was found in Yunnan Province near the site where the similar but slightly later *Psarolepis* was found. China, Early Devonian, 419–418 Ma.

Gundi see **Ctenodactylidae**.

Gunflintia a genus of cyanobacteria that is among the earliest-known bacteria. Around 2 billion years ago, it and similar photosynthetic organisms began to increase the oxygen content of the atmosphere to levels that supported more com-

plex life forms. First found in the 1950s in the Gunflint Chert of Canada and later in Australia, Proterozoic to Cambrian.

Gurbanodelta kara a species of basal metatherian mammals described in 2016, probably in the order Deltatheroida. Known only from a jaw fragment, it was a scansorial omnivore. Dated 10 million years later than the previously known deltatheroidans, it may be a Lazarus taxon if confirmed. Xinjiang, China, late Paleocene.

Gymnarthridae a family of microsaurian lepospondyl amphibians. They were relatively slender, with very small limbs and a single row of conical teeth. North America and possibly Europe, Late Carboniferous to early Permian.

Gymnocodiaceae an enigmatic family of small algae-like organisms, characterized by irregular tubes with perforate walls. They are sometimes classified as rhodophytes and sometimes as chlorophytes. Europe, North and South America, Asia, and Africa; Permian to Cretaceous.

Gymnolaemata a class of bryozoans that includes most living bryozoans; global distribution, Middle Ordovician to Recent.

Gymnophiona see **caecilians.**

Gymnosperms an extant group of seed-bearing plants that includes cycads, conifers, and ginkgos. Gymnosperms bear "naked" seeds, not enclosed in an ovary or seed-case as with angiosperms. They appeared in the tropics in the Late Devonian and rapidly spread worldwide. Global distribution, Late Devonian to Recent.

Gymnure see **Erinaceidae.**

Gyracanthus a genus of acanthodian fish in the family Gyracanthidae, considered either an acanthodian or a selachian, a true shark. From 2 to 3 feet long, *Gyracanthus* is notable for its fin spines, which were up to 18 inches long. Global distribution, Early Carboniferous.

Gyrogonites the fossil cast of the nucule, the female reproductive structure, of charophytes. The worldwide distribution and spiral ornamentations of these small, nutlike casts make them important index fossils in some freshwater deposits. Gyrogonites appear in the fossil record as far back as the Silurian.

H

Haasiophis a monospecific genus of marine snakes in the suborder Serpentes and family Simoliophiidae. About 3 feet long, *H. terrasanctus* is especially notable for still having hindlimbs, including partial feet. Known from an almost complete skeleton, it figures prominently in the ongoing debate about the origins of snakes. Israel, Late Cretaceous, 94 Ma.

Haast's eagle see ***Harpagornis moorei***.

Habelia optata a species of small chelicerate arthropods known only from the Burgess Shale, formerly thought related to crustaceans. *Habelia* was an inch long, but half of that length is the tail; it had chelicerae in front of the mouth, five pairs of walking legs, and sharp spines around its body. Canada, middle Cambrian.

Habrohagla a genus of katydid-like orthopteran insects in the family Prophalangopsidae (which was formerly called Haglidae); synonym *Parahagla*. *H. curtivenata* was 4–5 inches long and was very similar to the larger species of modern katydids. China and Russia, Early Cretaceous.

Hadrocodium wui a species of mouselike primitive mammal that has the earliest-known example of several mammalian ear and brain features. It is known only from a single skull, from which the body is estimated to have been about 1 inch long. China, Early Jurassic, 195 Ma.

Hadrosauridae a family of ornithischian duck-billed dinosaurs, one of the most successful dinosaur families, persisting from 86 to 66 Ma. Descendants of the iguanodontids, the hadrosaurs are divided into five subfamilies, the largest of which are the Lambeosaurinae and the Saurolophinae. Middle-sized herbivores, hadrosaurs ranged in length from 18 to 54 feet. North and South America, Europe, Asia, and Antarctica. Late Cretaceous, 86–66 Ma.

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Hagenowia a genus of atelostomate sea urchins, irregular euechinoids in the order Holasteroida and family Holasteridae. See ***Infulaster-Hagenowia*** **lineage**. Europe, Late Cretaceous, 89–66 Ma.

Hagen-Vorhalle site a Konservat-Lagerstatten in northwest Germany. An important site for insects from the beginning of the Pennsylvanian, it is known especially for arachnids, trigonotarbids, and eurypterids. It has produced well-preserved specimens of an almost complete eurypterid and of several giant dragonflies, especially *Namurotypus sippeli* and *Erasipteroides valentini*. Germany, Late Carboniferous, 325 Ma.

Hagerman Fossil Beds an important late Pliocene site in southern Idaho, in cliffs on the southwest bank of the Snake River. The site contains many mammals and other remains from the period about 3.7–3.2 Ma, notably the Hagerman horse, *Equus simplicidens*, which resembled a small zebra, about 4 feet high at the shoulder and weighing about 900 pounds. United States, Pliocene.

Haglidae see **Habrohagla**.

Hahnodontidae a family of small mammaliaforms formerly considered multituberculates but in 2018 placed in the order Haramiyida. Known only from four specimens from Morocco (*Hahnodon* and *Denisodon*) and Utah (*Cifelliodon*), they present features both of early mammaliaforms and of mammals. Africa and North America, Early Cretaceous, 145–125 Ma.

Haikouella a genus of primitive animals in the family Haikouellidae, found in the Chengjiang biota. Considered a probable chordate, it is similar to *Yunnanozoon* and also to *Pikaia* of the Burgess Shale. China, early Cambrian, ca. 518 Ma.

Haikouichthys a monospecific genus of primitive proto-vertebrate animals from the early Cambrian. About an inch long, it resembles a narrow *Myllokunmingia*. China, early Cambrian.

Halitheriinae a paraphyletic subfamily of sirenian mammals in the family Dugongidae. The type genus *Halitherium* is very similar to modern dugongs. North and South America, Africa, and Europe; early Oligocene to Miocene.

Halkieria a genus of enigmatic Cambrian organisms tentatively considered mollusks. In appearance like an armored slug, the halkieriids somewhat resemble *Wiwaxia*. They are generally 2–3 inches long and flattened, in the shape of an elongated oval. Known primarily from *H. evangelista* of the Sirius Passet site in Greenland but also found in Europe, Asia, and Australia; early to middle Cambrian.

Hallautherium schalchi a putative genus of stem-mammaliaforms in the clade Morganucodonta. Known only from a single double-rooted tooth found near Hallau, Switzerland. Late Triassic, 206–202 Ma.

Hallopora a large genus of "branching twig" stenolaemate bryozoans in the extinct order Trepostomata and family Halloporidae. The *Hallopora* are characterized by their dendroid habit, large pores, and many diaphragms in some branches. Bushy zoaria up to a foot across are seldom preserved intact, but the branches are important constituents of some reefs, especially Ordovician. Several species are index fossils. Global distribution, Ordovician to Devonian.

Hallucigenia one of the famous genera of the Burgess Shale, now known also from cousins in China and elsewhere. It may be related to modern velvet worms (Onychophora) and to *Collinsium ciliosum*, a late Cambrian worm. Some have suggested it as a basal arthropod. *Hallucigenia* is notable for 14 spikes on its back, 14 limbs, and a bulbous head with 2 eyes and a mouth encircled by a ring of small stiffening spikes; there are also teeth farther down its throat. North America, Europe, and Asia; early to middle Cambrian.

Hallux the proximal digit of the pes of vertebrates.

Halobia the largest genus of the Triassic oyster family Halobiidae; almost global distribution from Middle to Late Triassic.

Halobiidae a family of bivalves in the order Ostreoida and extinct superfamily Posidonioidea. Stratigraphically important in the Middle to Late Triassic, the family includes the genera *Aparimella*, *Daonella*, *Enteropleura*, *Halobia,* and *Taimyrolobia.* Widespread in the Tethys, Arctic, and Panthalassic Oceans, they are known from Eurasia and North America. Probably restricted to the Triassic.

Halocyprida one of the two accepted orders of ostracods in the subclass Myodocopa. Poorly known, they are generally subrectangular and have slight differences in appendages from the other order, the Myodocopida. Global distribution, at least from the Devonian to Recent.

Halszkaraptor escuilliei a species of basal dromaeosaurid dinosaurs in the subfamily Halszkaraptorinae. About 2 feet long with a long neck and tail, it seems to have been semiaquatic, with swimming and piscivorous features. It is one of very few dinosaurs that are possibly semiaquatic; see also ***Spinosaurus*** and ***Baryonyx***. Mongolia, Late Cretaceous, 70 Ma.

Halticosaurus a possible genus of dinosaurs, once suggested as synonymous with *Liliensternus* but now considered a dubious genus.

Halysitidae a family of chain corals in the order Tabulata. Colonies ranged from 2 inches to several feet wide, with the corallites connecting to each other in a strikingly chain-like pattern. Global distribution, Early Ordovician to Early Devonian, 472–412 Ma.

Hamipterus a genus of pteranodontoid pterosaurs in the suborder Pterodactyloidea. *Hamipterus tianshanensis* is notable for the discovery of hundreds of its eggs in Northwestern China; up to 1 inch long, the eggs are better preserved than most pterosaur eggs, and more than a dozen embryos have been identified. The species may have been colonial, but its social behavior is unclear since the discovered sites are allochthonous, with no nests. Like the few other pterosaur eggs found so far, these are similar to those of modern lizards, soft and flexible, lacking the calcium carbonate of the hard-shelled eggs of dinosaurs, birds, and crocodiles. China, Early Cretaceous, 120 Ma.

Hamites a paraphyletic genus of heteromorph ammonoids in the order Ammonitida and suborder Ancyloceratina. Named for the hook shape of most species, it has a very evolute, spirally shaped shell. Because of the drag created by the open shape, it was probably a relatively weak swimmer. Global distribution, Early to Late Cretaceous.

Hamulina a genus of heteromorph ammonitid ammonoids in the family Hamulinidae, notable for its unusual crook-shaped shell; Caribbean and Europe, Early to Late Cretaceous.

Hangenberg Event an extinction event dated at about 359 Ma, at the end of the Famennian, the final age of the Devonian. It is notable for widespread anoxia in the oceans.

Hanson Formation an important rock formation in the Central Transantarctic Mountains, important for an Early Jurassic fauna, especially dinosaurs, whose evolution in the period is poorly known. See ***Glacialisaurus*** and ***Cryolophosaurus***.

Haootia quadriformis a species of Ediacaran organisms considered by some to be early cnidarians, the earliest-known animal with muscles. Its body has a four-sided symmetry and is composed of bundles of muscles stacked horizontally, with short extensions from the corners. Newfoundland, Canada, Ediacaran, 560 Ma.

Haplocheirus sollers *a* species of avetheropod dinosaurs that seems to be the earliest-known member of the lineage of dinosaurs that led to birds. Known from only one specimen, it is the earliest and largest known of the superfamily Alvarezsauroidea. About 7 feet long in the body, it had a long tail, powerful biceps and forelimbs, and three long digits on the manus. Xinjiang, China; Late Jurassic, 160 Ma.

Haplohippus a genus of horses in the extant family Equidae and the subfamily Hyracotheriinae. A perissodactyl ungulate known from Oregon and Texas, *Haplohippus* was a forest browser. United States, late Eocene.

Haploid single or simple. Haploid cells are gamete (reproductive) cells that contain one set of genes or chromosomes rather than the two sets of diploid cells. In fertilization, haploid gametes combine to make a diploid, producing a zygote, a fertilized ovum.

Haplolepis a genus of small palaeoniscid actinopterygian fish in the family Haplolepidae. Like its relative *Canobius*, a smaller ray-finned fish of the Early Carboniferous, it had vertical jaw suspension and a large gape. It is named for its unusually straight rows of scales. United States and Europe, Late Carboniferous.

Haplorrhini "simple nose," a suborder of primates that includes humans, apes, monkeys, and tarsiers, as well as their extinct primate ancestors. The Haplorrhini are actually called "dry-nosed" in reference to their lacking a rhinarium, the moist area around the nostrils of the Strepsirrhini and most other mammals. Paleocene to Recent.

Haramiyavia a genus of synapsids in the clade Cynodontia. Small and probably insectivorous, it is known from jawbone and teeth fragments from the end of the Triassic, 30–40 million years earlier than the earliest definitive mammals. Greenland, Late Triassic, 210 Ma.

Haramiyidae an enigmatic family of protomammals of the Late Triassic. The haramiyids are generally considered not true mammals but part of a side branch of mammaliaform animals that became extinct at the end of the Cretaceous. North America, Europe, Asia, and Africa; Triassic to Cretaceous.

Hardground a layer of sediment precipitated by calcium carbonate just below the surface of the sea floor.

Hard parts mineralized or otherwise hardened structures of an organism that fossilize easily, such as shells, bones, horns, bills, teeth, cuticles, claws, and scales.

Harpagornis moorei Haast's eagle, a large predator of New Zealand that became extinct only 500–700 years ago, after the arrival of humans on the two islands. Weighing 22–40 pounds, it had a 9 foot wingspan and was at least 30% larger than the largest modern bird of prey. Some genetic research suggests that it is most closely related to a very small bird of prey, the 2 pound *Hieraaetus* eagle of Australia and New Guinea. The probable common ancestor of *Harpagornis* and *Hieraaetus* is another 2 pound species that lived between 1.8 and 0.7 Ma, so that *Harpagornis* represents one of the most rapid instances of island gigantism. Before the arrival of

humans, the only mammals in New Zealand were three species of bats, but there were 250 species of birds. *Harpagornis* dominated the food chain, hunting the 400 pound moas (Dinornithidae); both went extinct within a century of the arrival of humans and accompanying rats, which multiplied in the absence of natural predators and ate the eggs of many birds.

Harpetida an order of trilobites, included in the proposed subclass Librostoma. They have an unusual brim around the cephalon, probably a feeding apparatus, that kept the animal from enrolling tightly. They are also characterized by very small eyes and flat genal prolongations. Global distribution, late Cambrian to Late Devonian.

Harpoceras a genus of ammonoids in the family Hildoceratidae. Generally thin-shelled and flattened laterally, the various species range widely in size, from 5 inches up to 18 inches high. Global distribution, Early to Late Jurassic.

Harpymimus okladnikovi a species of ornithomimosaurian dinosaurs in the family Harpymimidae. Known from an almost complete skeleton 7 feet long, it was partially toothed and is considered a basal ornithomimosaurian. The more derived ornithomimosaurians developed a beak and were toothless. See also ***Pelecanimimus***. Mongolia, 109–100 Ma.

Harvestman see **Opiliones.**

Hatzegopteryx a genus of very large azhdarchid pterosaurs in the suborder Pterodactyloidea, known from fragments found in Romania. It is estimated to be as large as *Quetzalcoatlus*, to which it is similar, both of them having a wingspan of about 40 feet. Romania, Late Cretaceous, 66 Ma.

Hebertella a genus of rhynchonellate brachiopods in the order Orthida and family Plectorthidae; type species: *Orthis sinuata*. Articulate and impunctate, its massive shell is 1.2 inches wide, with fine radial ribbing. The pedicle valve is slightly convex with a fold, and the brachial valve was strongly convex. Global distribution, Early Ordovician to early Silurian.

Hedgehog see **Erinaceidae.**

Heidelberg man see ***Homo heidelbergensis*.**

Helaletes a genus of lophiodont tapirs in the superfamily Tapiroidea and extinct family Helaletidae. Derived from *Homogalax* and close to the ancestry of the modern tapir, *Helaletes* was small and agile and looked like a small horse. North America and Asia, early Eocene, 50–46 Ma.

Helcionelloida an early Paleozoic class of small marine mollusks, characterized by rugose, cap-shaped shells, conical and sometimes coiled; global distribution, early Cambrian to Early Ordovician.

Helens a pair of long, curved, calcareous extensions often found connected to the operculum of hyoliths. The function is unclear, perhaps as supporting structures; it was named for C.D. Walcott's wife and daughter.

Heliconiinae an extant subfamily of butterflies in the superfamily Papilionoidea and family Nymphalidae. The group is well-known for examples of Batesian and Müllerian mimicry. Miocene to Recent.

Helicoplacus "spiral plate," an unusual genus of early echinoderms in the class Helicoplacoidea. It is one of the earliest echinoderms but is represented by only two species and very few specimens. *Helicoplacus* had a thick, cigar-like shape and was 2–3 inches high, with spirally arranged plating on three ambulacra, different from other echinoderms in lacking pentameral symmetry. The only complete specimen was found in the White Mountains of California, but fossil plates have been found across North America. Early to middle Cambrian.

Helicoprion a genus of eugeneodontiform holocephalian fish in the family Agassizodontidae. Shark-like and estimated between 12 and 25 feet long, it is known only from heterodont teeth and partial skulls since the cartilaginous body disintegrated soon after death. *Helicoprion* is notable for its dentition, with a tooth-whorl as a cutting plate in the lower jaw and simple crushing teeth in the upper jaw. The tooth-whorl consisted of a single continuous row of inwardly curving teeth, containing as many as 150 sharp teeth. Global distribution, middle Permian, 285–270 Ma.

Heliolites a diverse genus of colonial tabulate corals in the family Heliolitidae. Each of its circular corallites, evenly spaced from each other over the surface of the colony, has 12 segments. Global distribution, Middle or Late Ordovician to Late Devonian.

Heliomedusa a monospecific genus of early brachiopods in the family Discinidae. Circular and less than an inch in diameter, *H. orienta* was first thought a jellyfish, but it is now known from dozens of specimens in the Chengjiang biota that show the lophophore and the growth lines of the shell. China, early Cambrian, ca. 518 Ma.

Hell Creek Formation an important North American formation that comprises strata from the end of the Cretaceous and beginning of the Paleocene, dated roughly 70–65 Ma. With the Frenchman Formation of Saskatchewan, its outcrops occur in a circular area 600 miles in diameter, centered in northeastern Montana. It is best-known for dinosaur fossils, including the most complete hadrosaur skeleton and

several almost complete skeletons of ***Triceratops*** (*q.v.*) and *Tyrannosaurus rex*. The formation has also produced fossils of invertebrates, plants, fish, reptiles, pterosaurs, amphibians, and birds. Near its boundary with the overlying Fort Union Formation, there are exposures of the iridium-enriched stratum that marks the end of the Mesozoic Era. See also **Turtle Graveyard**.

Helminthoidea a group of ichnofossils generally interpreted as traces of worms. They are often found as long burrows, separate but closely spaced and often parallel. A common species is called *H. labyrinthica* for the labyrinthine pattern in some specimens. See also **Aberystwyth**; cosmopolitan, Silurian to Recent.

Helodontidae an enigmatic family of holocephalic fish, grouped with the Chimaeriformes, possibly related to sharks. The type genus is *Helodus*. About a foot long, the Helodontidae had a low heterocercal tail fin. Instead of toothplates, they had a series of flattened tooth elements in each jaw. Australia, North America and Europe; Late Devonian to Permian.

Helohyidae "marsh pig," a family of small palaeodont artiodactyl mammals. They were similar to the Raoellidae and possibly close to the ancestry of whales. Asia and United States, late Eocene to late Oligocene.

Hemichordata an extant phylum of soft-bodied marine deuterostomes. Closely related to echinoderms, they are wormlike filter feeders, ranging in length from 1 inch to 6 feet. The phylum includes two principal classes, the Enteropneusta and the Pterobranchia. Global distribution, early Cambrian to Recent.

Hemicidaris a genus of echinoids in the order Hemicidaroida and family Hemicidaridae; Europe, Africa, and United States; Middle Jurassic to Early Cretaceous.

Hemicidaroida a paraphyletic order of sea urchins, regular echinoids in the subclass Euechinoidea; cosmospolitan, Late Triassic to Late Cretaceous.

Hemicrinus an unusual genus of crinoids in the order Cyrtocrinida and family Hemicrinidae. It had a spoon-like cup set at a right angle to a strong stalk, attached to a holdfast in shallow water. Europe, Early Jurassic to Early Cretaceous.

Hemicyclaspis a genus of osteostracan fish in the order Atelaspidiformes, closely related to *Cephalaspis*. From 4 to 5 inches long, it was pleuronectiform and is characterized by paired pectoral fins, a low dorsal fin, a row of low dorsal spines, a single nostril, and a bony headshield that was almost circular in cross-section. Canada and Europe, Early Devonian.

Hemicyoninae a subfamily of carnivorous ursid mammals that probably includes the ancestors of modern bears. The later species, such as *Hemicyon*, ranged from 4 to 7 feet long and were generally digitigrade. North America, Europe, and Asia; late Oligocene to late Miocene.

Hemipneustes a sea urchin, a genus of large irregular euechinoids in the order Holasteroida and family Holasteridae. With a high-domed test and a deeply sunken anterior ambulacrum, it was the largest echinoid of the Cretaceous. Europe and Asia, Early to Late Cretaceous.

Hemipsalodon "semi-shearing teeth," a genus of creodonts in the family Hyaenodontidae. A scavenging carnivore, *H. grandis* was 6–7 feet long and weighed about 250 pounds. Its first and second molars were carnassial, modified for slicing meat. Western North America, late Eocene.

Hemizonida an order of primitive sea stars, echinoderms in the class Asteroidea; North America and Europe, early Silurian to Late Carboniferous.

Henodus chelyops an enigmatic species of placodont reptiles in the family Henodontidae. Known only from a lagoon fossil site in southwestern Germany, *Henodus* is one of the later placodonts that developed turtle-like armor against predators. It had a plastron and a broad, almost circular carapace, fused to its vertebrae and covered with a mosaic of ossicles and scutes. About 3 feet long, *Henodus* differed also from earlier placodonts in being almost toothless, and it is thought to have been a filter feeder, using a set of bristles and denticles to strain food from the fresh- or brackish-water lagoon. Germany, Late Triassic.

Heptodon a genus of perissodactyl placental mammals in the superfamily Tapiroidea and family Helaletidae. About 3 feet long, it closely resembled its coeval relative *Helaletes* and the modern tapir. North America and Asia, early Eocene, 55–49 Ma.

Hercynian orogeny see **Variscan orogeny**.

Herefordshire Nodules a Silurian assemblage of carbonate nodules from a volcanic ash stratum of the Wenlock Series dated between 427 and 425 Ma. The nodules contain exceptionally preserved calcitic fossils of organisms of a shallow epicontinental sea, including brachiopods (see ***Bethia***), polychaete worms, mollusks, crustaceans (see ***Colymbosathon*** and **Myodocopa**), and echinoderms. Since the fossils cannot be separated from their matrix and splitting the nodules produces little information, many have been digitally recorded by a complex process of serial thin sectioning by grinding and digitally photographing the series of sections. The resulting digital records constitute an unusual Konservat-Lagerstatten. Western England, late Silurian.

Herodotius see **Macroscelidea**.

Herpetotheriidae a large family of metatherian mammals, generally considered a sister group to modern marsupials. Widespread in the Paleogene, they were probably ground-dwelling omnivores. Genera include *Armintodelphys*, *Amphiperatherium*, *Asiadidelphis*, *Herpetotherium*, and *Peratherium*. North America, Europe, North Africa, and Asia; Late Cretaceous to Miocene.

Herpetotherium a genus of marsupials in the family Herpetotheriidae, widespread in North America from the early Eocene to early Miocene. *Herpetotherium* was a small ground-dwelling omnivore, closely related to modern marsupials. North America, Eocene to Miocene.

Herrerasauridae a family of early saurischian dinosaurs. They are traditionally considered theropods, but 2017 research argues that their similarities may be simply the result of convergent evolution rather than phylogenetic relationship. The carnivorous herrerasaurids were relatively small dinosaurs, generally less than 15 feet long. South and North America, Late Triassic, 231–215 Ma.

Herrerasaurus a genus of early saurischian dinosaurs in the carnivorous family Herrerasauridae. The type species, *H. ischigualastensis*, is dated at 231 Ma; lightly built, its length is estimated at between 10 and 15 feet and its weight up to 700 pounds. It has been variously classified as a theropod or a sauropodomorph. Ischigualasto Formation, Argentina, Late Triassic.

Hesperocyon a genus of basal North American canids. Possibly ancestral to all later canids, *Hesperocyon* was almost 3 feet long but lightly built, weighing less than 5 pounds. It is known from Saskatchewan to Colorado, middle Eocene to early Oligocene.

Hesperocyoninae a disputed subfamily of early North American canids. Generally considered the descendants of *Hesperocyon*, the subfamily contains about ten genera of small canids, including *Cynodesmus* and *Mesocyon*. North America, middle Eocene to middle Miocene.

Hesperornis the best-known member of the hesperornithine birds, a more advanced early group than the Enantiornithes. *Hesperornis* was a large, flightless, diving sea bird, almost 6 feet long. North America and Asia, Late Cretaceous, 85–75 Ma.

Hesslerides a genus of trilobites in the family Proetidae. *Hesslerides* is especially characterized by a large glabella comprising most of the cephalon, with crescentic eyes set near the rear of the cephalon. United States, Early Carboniferous.

Heteractinida a probably paraphyletic Paleozoic order of sponges in the extant class Calcarea, with six- or eight-pronged calcareous spicules. Global distribution, early Cambrian to Carboniferous.

Heterobranchia a subclass of gastropod mollusks that includes the opisthobranchs (mostly marine snails and some shell-less forms such as the nudibranchs) and the pulmonates (most terrestrial snails and slugs as well as some freshwater and marine snails). See also **Mathildoidea**. Global distribution, Carboniferous to Recent.

Heterocercal referring to an asymmetrical tail fin, generally with the upper part extending farther than the lower part, seen especially in sharks. On the other hand, the Anaspida and at least some mosasaurs have a reversed heterocercal tail fin.

Heterochrony a genetic shift in the evolutionary development of tissue or an anatomical part, causing it to develop at an abnormal time relative to an ancestor. The change can then be inherited by the offspring. For example, the adults of some later species of the Jurassic bivalve genus *Gryphaea* exhibit traits that were juvenile in an earlier species.

Heterocorallia a small suborder of late Paleozoic corals, generally considered part of the order Rugosa. The genera of the single family, the Heterophyllidae, are solitary and elongate, with an axial branching arrangement of protosepta and septa. Global distribution, mainly Early Carboniferous (Middle Devonian to Early Pennsylvanian).

Heterocrania rhyniensis a species of arthropods in the subclass **Euthycarcinoidea**, *q.v.*; Scotland, Early Devonian.

Heterodont dentition having more than one type of teeth (such as canines, incisors, premolars, and molars) evidence of specialization in feeding.

Heterodontosauridae a basal family of ornithischian dinosaurs; a long-lived and widespread group known from sparse specimens on all continents except Australia and Antarctica. They were as long as 6 feet, with a long tail and long, grasping forelimbs. They are named for their heterodont dentition, having three different types of teeth. They were generally herbivorous, but some also preyed on small animals. Only *Heterodontosaurus* is known from a complete skeleton, but see also ***Abrictosaurus***. Late Triassic to Early Cretaceous.

Heterodontosaurus a monospecific genus of ornithischian dinosaurs. It is known from several specimens but primarily from an articulated skull and skeleton dated between 210 and 190 Ma. *Heterodontosaurus* was up to 6 feet long, had three different types of teeth, and had five digits on the manus and four on the pedes. South Africa and North and South America, Late Triassic to Early Jurassic.

Heteromyidae an extant family of rodents in the superfamily Geomyoidea. Widespread in North America in the Oligocene, the family's range has shrunk, but the kangaroo mouse and kangaroo rat are two of many surviving genera. North and Central America, Oligocene to Recent.

Heteronectes a genus of flatfish showing a transitional stage in the development of flatfish asymmetry. See also **flatfish.** Known only from France, middle Eocene.

Heterosoricinae a proposed subfamily of insectivores in the family Soricidae (the shrews); North America, Europe, Africa, and Asia; Eocene to Pliocene.

Heterospory the production of two types of spores differing in size and sex. Heterospory is known in several types of terrestrial plants such as *Archaeopteris* and the club mosses in the Devonian.

Heterostraci a diverse subclass of fish-like vertebrates in the class Pteraspidomorphi. Jawless, armored, generally small (5–9 inches), and benthic, they evolved at a time when mineralized skeletons were first appearing in the fossil record. The group includes principally the cyathaspids and their descendants the pteraspids. The last of the heterostracans were the Psammosteidae, extinguished at the end of the Devonian. Global distribution, late Cambrian to Late Devonian.

Hexacorallia the large subclass of Anthozoa that includes the sea anemones (Actiniaria) and the corals (Scleractinia, Rugosa, Tabulata, and Antipatharia).

Hexactinellida a class of glass sponges with four-, five-, and six-rayed siliceous spicules; formerly called Hyalospongiae**.** They are more common as fossils than demosponges because their siliceous spicules fossilize easily. Global distribution, Cambrian to Recent.

Hexanchiformes an extant order of primitive sharks in the superorder Squalomorphii. Generally considered the earliest sharks, hexanchiforms are characterized by six or seven gills, one dorsal fin, and a heterodont dentition. They are well-known from the Middle Jurassic through the Cenozoic, and, in addition, teeth resembling those of hexanchiforms are known as far back as the Devonian. The extant families are the Hexanchidae and the Chlamydoselachidae, and extinct families are the Crassonotidae, Mcmurdodontidae, and Orthacodontidae. Global distribution, Devonian to Recent.

Hexapoda a subphylum of arthropods that in addition to the true insects includes the proto-insects in the class Entognatha (the Collembola, Protura, and Diplura). The group has also traditionally included myriapods, but genetic evidence may exclude them. Global distribution, Early Devonian to Recent.

Hexathelidae see ***Rosamygale***.

Heymonsicambria scandica one of several important discoveries of fossil pentastomes showing that the parasitic **Pentastomida** (*q.v.*), tongue-shaped worms, date back to the Cambrian; Canada, late Cambrian.

Heyuannia a genus of theropod dinosaurs in the family Oviraptoridae. Growing up to 5 feet long and 50 pounds, *Heyuannia* had a short, toothless beak, a low crest, and very short forelimbs. Known from several skulls and partial skeletons, it is especially significant for its eggs, which were laid in partly open nests and contain two pigments similar to those in the eggs of modern birds. China, Late Cretaceous, 70 Ma.

Hiemalora a poorly known genus of Ediacaran fossils, known best from the Mistaken Point fauna. *Hiemalora* is a tentacular medusoid, resembling a sea anemone, with 12–20 arms radiating from a 2 inch circular body. It has been suggested as a stem-anthozoan. Canada, Russia, and Australia; Ediacaran, 575–560 Ma.

Hildoceras a genus of ammonoids in the order Ammonitida and family Hildoceratidae. Characterized by a narrow, discoidal, and evolute shell, *Hildoceras* is named for St. Hilda, the founding abbess of Whitby Abbey in Yorkshire, England, who legendarily turned all the snakes into stone, creating the ammonoids. Europe and Asia, Middle Jurassic, 183–174 Ma.

Himerocrinus a genus of large pelmatozoan crinoids in the subclass Camerata and order Monobathrida. Poorly known but probably related to *Dolatocrinus, Himerocrinus* was one of the largest crinoids, with a calyx 4–6 inches wide and up to 80 branching arms. United States, Devonian.

Hindeodus parvus a species of conodonts in the family Anchignathodontidae. Its first appearance marks the beginning of the Mesozoic Era and the Triassic Period at 252.17 Ma. China.

Hipparion a widespread genus of horses in the subfamily Equinae. Much larger than *Merychippus*, it stood almost 5 feet high at the shoulder and weighed between 240 and 270 pounds. It had two vestigial toes on either side of the hoof and not touching the ground. Appearing around 20 Ma, *Hipparion* migrated rapidly over most of the world. North America, Europe, Asia, and Africa; early Miocene to middle Pleistocene.

Hippuritida the rudists, an order of euryhaline bivalve mollusks in the class Heterodonta; also spelled Hippuritoida. Flourishing in the warm, saline water of the Cretaceous, they became the basis of the most prominent reefs of the period, cementing themselves together in tropical reefs several hundred feet high, which ran for hundreds of miles along some Cretaceous coastlines. They took various tube and conical shapes, the latter sometimes as long as 40 inches; see, for example, ***Radiolites***. Cosmopolitan, Late Jurassic to the end of the Cretaceous.

Hirnantian fauna a unique fauna dominated by brachiopods, dated near the beginning of the Hirnantian Age, 445 Ma. It was short-lived but almost worldwide, lasting until the end-Ordovician extinction at 443.8 Ma.

Holarctic referring to the Holarctic Region, the temperate areas of Europe, Asia, North America, and North Africa, from the Late Jurassic to the present.

Holaspis the final ontogenetic phase of trilobites, followed by several molts that merely increased body size and added segments; see also **meraspis** and **protaspis**.

Holasteroida an order of Mesozoic sea urchins, heart-shaped atelostomate echinoderms. Several species are important in biostratigraphy, with a few genera still extant. Early Cretaceous to Recent.

Holectypidae a family of irregular echinoids in the order Holectypoida. The group includes some of the earliest and most primitive irregular echinoids, similar to the Pygasteridae. Global distribution, Early or Middle Jurassic to Late Cretaceous.

Hollinoidea a superfamily of dimorphic paleocopid ostracods in the suborder Beyrichicopina. Some forms have sulci and lobation. North America and Europe, Devonian to Permian.

Holmesina see **Pampatheriidae**.

Holocene the most recent epoch of the Cenozoic Era, the last 11,700 years.

Holocephali an extant subclass of cartilaginous fish in the class Chondrichthyes. Known as far back as the Devonian but only from scattered teeth, the only surviving order is the Chimaeriformes, the ghost sharks. Global distribution, Devonian to Recent.

Holochroal the type of compound eye in most trilobites, with thousands of tightly packed lenses covered by a single cornea; see also **schizochroal**.

Holocrinidae a family of crinoids in the order Isocrinida; North America and Eurasia, Early to Late Triassic.

Holocrinus a genus of isocrinid crinoids in the family Holocrinidae. One of the earliest post-Paleozoic crinoids, *Holocrinus* was stalked but probably able to move from place to place on the substrate. The United States, Europe, Asia, and New Zealand; Early to Late Triassic, 251–237 Ma.

Holoptychiidae a family of sarcopterygian fish in the order Porolepiformes. These lobe-finned fish included at least one genus that may have been amphibian, *Laccognathus*. North America and Europe, Middle Devonian to Early Pennsylvanian.

Holopus an extant genus of crinoids in the order Cyrtocrinida and family Holopodidae. It attaches itself to deep-sea substrate, sometimes on the underside of rocks. In a significant difference from other cyrtocrinids (almost all of which are passive suspension feeders), its five stout arms probably capture small fish; when they are closed, *Holopus* looks like a squat, tubercular mushroom. Its fossil record is sparse, but it probably originated in the Paleocene. Known mainly from the Arctic, it is found only in deep, cold water.

Holostei an extant, possibly paraphyletic infraclass of non-teleost neopterygian fish. Their skeleton is cartilaginous but covered with a layer of bone, and their scales are ganoid. They were abundant in the Mesozoic but have declined since then. Living representatives are the bowfins of the order Amiiformes and the gars of the order Semionotiformes. Late Triassic to Recent.

Holothuroidea the sea cucumbers, an extant class of echinoderms in the subphylum Echinozoa. Their cylindrical body is covered by a leathery skin which contains ossicles of different types and sizes. They are generally 6–12 inches long, but the longest known (*Synapta maculata*) grows to 10 feet. They are benthic, most of them able to move on the sea floor by means of tube feet. The fossil record is poor since there is no integrated skeleton, but ossicles and elements of the calcareous ring around the mouth are known from as early as the Silurian, and body specimens are known from the Devonian and later. Global distribution, Silurian to Recent.

Holotype a single physical specimen of the type species of a taxon, designated as the defining type of the taxon at the time when it is formally described and established as a formal group. The holotype anchors specific physical characters to the name of the taxon.

Holurus a genus of chondrostean fish in the family Palaeoniscidae, distinguished by an ossified exoskeleton and robust rhombic scales; Europe, Early Carboniferous to Permian.

Holzmaden Shale a Lower Jurassic Konservat-Lagerstatten in Southern Germany, where several limestone and shale quarries have produced exceptionally preserved specimens of shallow-sea taxa from the *Posidonia* Shale formation, dated at 185–183 Ma. Of the vertebrate fossils, the most common are the ichthyosaurs, including a *Stenopterygius* with a dorsal fin and an upper lobe of the tail. Many of these specimens show stomach contents, and there is a high percentage of juveniles and females with unborn fetuses, indicating that the area was probably a spawning ground. Other vertebrates include teleosaurid crocodiles (see ***Steneosaurus***), pterosaurs, and fish. Cephalopods such as the ammonoid *Harpoceras* are common, and other invertebrates include crinoids and bivalves. It is one of three Lagerstätten dated near 183 Ma; see also **Strawberry Bank** and **Ya Ha Tinda.**

Homacodontidae a paraphyletic family of palaeodont mammals in the superfamily Dichobunoidea, among the earliest and most generalized artiodactyls; North America, Asia, and Europe; Eocene.

Homalodotherium a genus of notoungulate mammals in the suborder Toxodonta. About 7 feet long and weighing 600–700 pounds, it was superficially more similar to the chalicotheres than to other toxodonts, with claws instead of hooves. Also, its forelimbs were digitigrade and hindlimbs plantigrade, indicating partial bipedality. South America, Miocene, 16 Ma.

Homalozoa a controversial group of early Paleozoic animals of uncertain affinities; formerly called Carpoidea and sometimes referred to as calcichordates or stylophorans. They are generally considered stem-group echinoderms and are thought by some to have an evolutionary link with chordates. Completely asymmetrical, they have a calyx with a short stem and projecting arm and taillike structures. See also **Homoiostelea**. Global distribution, middle Cambrian to Early Devonian.

Hominid term referring to the family Hominidae, which includes all modern great apes (i.e., modern humans, gorillas, chimpanzees, and orangutans) and their immediate ancestors; early Miocene to Recent.

Hominin term referring only to modern humans, extinct members of the genus *Homo*, and their immediate ancestors, such as *Australopithecus*, *Paranthropus*, and *Ardipithecus*; late Miocene to Recent.

Hominoidea the apes, a superfamily of haplorhine primates consisting of the families Hominidae and Hylobatidae; Oligocene to Recent.

Homocephale see ***Prenocephale***.

Homo erectus a species of primates more advanced in several ways than *H. habilis* and probably ancestral to *H. sapiens*. Remains of *H. erectus* have been found in Java, China, Africa, Europe, and Western Asia, some as old as 1.75 million years and some possibly as young as 70,000 years ago. *Homo erectus* was on average about 5 feet tall and had a cranial capacity slightly less than *H. sapiens*. Although it was long thought to be the first hominin to walk upright, other species, notably *Australopithecus afarensis*, now seem to have done so as early as 3.4 Ma. Several skulls and jawbones found in the Republic of Georgia, named *H. erectus georgicus*, have been dated at about 1.7 Ma and are similar to a jawbone from Kenya from 1.6 Ma; they are thought to be evidence of early migration of the species from Africa. Some authorities now divide *H. erectus* into three separate species in Africa, Europe, and Asia. See also **Denisovans**, **Neanderthals**, and **Ngandong fauna**.

Homo erectus pekinensis a form of *H. erectus* with a massive brow ridge and a cranial capacity of 900–1200 cc. Tools and the remains of modern humans have also been found at the site. Northern China, Pleistocene, about 750,000 years ago.

Homo ergaster the group of hominins considered by some to be the branch of *H. erectus* that gave rise to *H. sapiens* in Africa. See also **Turkana Boy. S**outheastern Africa, 1.9–1.3 Ma.

Homo floresiensis a species of hominins known from partial skeletons of nine individuals found on the Indonesian island Flores. Between 2 and 4 feet tall, the specimens have generated intense debate, some claiming that a disease caused their diminutive size. The emerging consensus, however, is that they do represent a separate species. Dated between 200,000 and 50,000 years ago.

Homo habilis possibly the earliest-known representative of its genus, *H. habilis* lived from about 2 million years ago to about 1.75 million years ago, with most specimens found in Africa and Asia. It is possibly ancestral to *H. erectus*, with a cranial capacity (around 650–700 cc), slightly more than that of the australopithecines but less than that of *H. erectus*.

Homo heidelbergensis a disputed species of hominins, considered by some to represent the branch of *H. erectus* that was ancestral to Neanderthals and modern humans. Germany, England, Ethiopia, Zambia, and possibly Asia; 600,000–120,000 years ago.

Homoiostelea a controversial class of early biradiate echinoderms, generally placed in the subphylum Homalozoa. They had a feeding arm and a stem consisting of a series of plates. Cosmopolitan, Cambrian to Devonian.

Homologous structures body parts of different organisms that have anatomical features in common but perform different functions. For example, bats' wings and human hands have homologous bone structures, but only bats can fly. The hindlimbs of whales may seem homologous with those of hippopotamuses; but since they are no longer functional, the whales' hindlimbs are considered vestigial. See also **analogous structures** and **vestigial structures.**

Homo naledi the name given to a species of hominins known only from a deposit of bones in a cave north of Johannesburg, South Africa, probably a burial site. Research in 2017 indicates a possible relationship to *H. habilis* or *H. erectus*, but, found in loose soil and unaccompanied by other fauna, the bones are difficult to date, with estimates ranging from 2.5 to 0.9 Ma. They represent parts of at least 15 individuals, and there are multiple examples of almost every bone in the body, so

that the skeleton constructed from them is more complete than that of any previously known hominin ancestor. This discovery seems to represent an early stage of hominin development: the brain is only the size of an orange, but there are other more advanced features.

Homo neanderthalensis see **Neanderthals**.

Homo rhodesiensis the name given to several pre-modern hominin specimens found in the twentieth century in East and North Africa. Dated between 400,000 and 120,000 years ago, the group is thought by some to be an African version of *H. heidelbergensis* and probably in the direct line of descent to *H. sapiens*.

Homo sapiens a species of primates including modern humans (*Homo sapiens sapiens*) and a few extinct subspecies. Although the oldest definitive fossils are from Eastern and Southern Africa and around 200,000 years old, a 2017 analysis of specimens found in Western Morocco indicates a date of origin of 300,000 years ago and distribution over the whole continent. According to a finding in Israel reported in 2018, the earliest evidence of *H. sapiens* outside Africa is a partial jawbone about 185,000 years old (see **Misliya**). See also **Jebel Irhoud, Cro-Magnon, Denisovans,** and **Neanderthal**. Middle Pleistocene to Recent.

Homostelea see **cinctans**.

Homotherium a genus of large felid mammals in the subfamily Machairodontinae. Its canines were longer than those of *Machairodus* but shorter than some other saber-toothed cats. *Homotherium* was about the size of a modern male lion, but its elongated forelimbs and short tail give it a hyena-like appearance. It seems to have lived in Europe up to 28,000 years ago. Global distribution except Australia, Pliocene to Pleistocene.

Honeycomb coral see **Tabulata**.

Hoolock an extant genus of apes in the gibbon family Hylobatidae; see also ***Bunopithecus***. India and China, Recent only.

"Hopeful monster" hypothesis a biological hypothesis that macroevolutionary changes result primarily from large mutations rather than from a succession of gradual microevolutionary steps. Although the original statement of the hypothesis by Richard Goldschmidt is discounted, genetic research in regulatory genes has revived interest in the basic idea. See also **uniformitarianism** and **punctuated equilibrium**.

Hoplitoplacenticeras a genus of Late Cretaceous ammonoids in the order Ammonitida. Its shell can be 2–3 feet high and so strongly ribbed that it has a spiky

appearance. Important stratigraphically in the Campanian, it is the latest representative of the Placenticeratidae. Global distribution from the Santonian through the Maastrichtian, 85–66 Ma.

Hoplopteryx a genus of teleost actinopterygian fish in the extant family Trachichthyidae, related to the modern roughy. Almost a foot long, it had relatively small fins, but the dorsal fin was supported by a row of strong spines. In an evolutionary advance, a series of uroneural bones in the tail supported the fin rays and made *Hoplopteryx* a strong swimmer. Global distribution, Late Cretaceous, 90–70 Ma.

Horizon in paleopedology, a layer of soil. The upper layers lie generally within 1.5 feet of the surface (labeled horizons A and E), and the subsurface horizon lies within 7 feet of the surface (labeled horizon B).

Horned dinosaur see **Ceratopsia.**

Horse *see* **Equidae**.

Horseshoe crab see ***Limulus***.

Horsetails see ***Equisetum***.

House Range see **Wheeler Shale.**

Huayangosaurus taibaii a genus of small basal stegosaurian dinosaurs. Known from several partial skeletons, *Huayangosaurus* is dated at about 20 million years earlier than *Stegosaurus*, which it resembles closely except for being much smaller, only 15 feet long. It had tall spiked plates on its spine, down to the terminal group of four tail spikes, and also had long shoulder spikes. China, Middle Jurassic, 172–161 Ma.

Hudsonaster a genus of sea stars, asteroids in the family Hudsonasteridae; synonym *Paleaster*. The upper surface is heavily plated with rounded ossicles. North America, Middle to Late Ordovician.

Hulettia a genus of teleost palaeonisciform fish in the clade Halecostomi. It was 4–5 inches long and notable for its robust ganoid scales, which protected it from predation. United States, Middle to Late Jurassic, 167–145 Ma.

Hunsrück Slate Several quarries in this Konservat-Lagerstatten of the Early Devonian (about 407 Ma) contain well-preserved soft-tissue pyritization fossils. Important examples include fish (especially *Drepanaspis* and *Gemündina*)**,** echinoderms (crinoids, asteroids, and ophiuroids), mollusks, and several arthropods (espe-

cially the malacostracan crustacean *Nahecaris* and the pycnogonid sea spider *Palaeoisopus*). Germany, Early Devonian, Pragian to Emsian Ages.

Hupehsuchia an order of neodiapsid marine reptiles tentatively placed in the clade Ichthyosauromorpha. The group is known from five species, all found in Hubei Province and dated between 250 and 246 Ma; the earliest is *Eohupehsuchus*, and the most derived is ***Eretmorhipis***, *q.v.* From 2 to 4 feet long, the hupehsuchians seem to represent a cross between ichthyosaurs and crocodilians. They are notable for an elongated skull, overlapping layers of dorsal osteoderms, paddle-shaped limbs, gastralia, and a long tail. China, Early to Middle Triassic.

Hurdia a genus of stem-arthropods in the order Radiodonta. Known first from the Burgess Shale assemblage and at first misidentified, in 2009 it was correctly described and seen to be related to *Anomalocaris*. Between 8 and 20 inches long, it is characterized especially by large gills suspended from lobes on its sides and by a thin, pointed carapace extending forward. Canada, Europe, and Asia; middle Cambrian.

Hutchemys a genus of soft-shell cryptodire turtles in the extant family Trionychidae. About 2 feet long, it is known in several species from the Western United States, Late Cretaceous to late Paleocene, 71–56 Ma.

Hyaenarctos see ***Agriotherium***.

Hyaenidae see **Ailuroidea**.

Hyaenodon a diverse genus of creodonts in the family Hyaenodontidae. The largest species, *H. gigas*, was about 10 feet long and weighed half a ton, and the smallest were fox-sized. Not a direct ancestor of the modern hyenas, the catlike *Hyaenodon* was digitigrade. North America, Europe, Africa, and Asia; late Eocene to middle Miocene.

Hyalospongiae see **Hexactinellida**.

Hybocrinida a small suborder of early crinoids generally placed in the order Cladida. Hybocrinids are distinguished by a monocyclic cup and circular stem. North America and Europe, Middle to Late Ordovician and possibly early Silurian.

Hybodontiformes "hump tooth," a long-lived suborder of euselachian sharks, named for their compressed conical teeth. Dominant Mesozoic predators, hybodonts, were 6–7 feet long. Prominent genera include *Hybodon* and *Ptychodus*, the type genera of the large families Hybodontidae and Ptychodontidae. Global distribution, Early Carboniferous to Late Cretaceous.

Hydnoceras a genus of glass sponges in the class Hexactinellida. Horn-shaped and about 8 inches long, it is an index fossil in the Late Devonian. North America and Europe, Devonian to Mississippian.

Hydrodamalis gigas Steller's sea cow, a genus of sirenians in the family Dugongidae. As long as 30 feet and weighing 11 tons, it was toothless and fed entirely on seaweed. With a very thick layer of blubber, it may have been unable to dive and was hunted to extinction in the middle of the eighteenth century. North Pacific Ocean, Pliocene to Holocene.

Hydrozoa a class of cnidarians in the subphylum Medusozoa. Mostly soft-bodied, predatory marine animals, solitary or colonial, they are generally small, with a body plan similar to that of sea anemones. They include the Portuguese man-of-war but are separate from the jellyfish (see **Scyphozoa**). They probably date back to the Precambrian, but fossils are rare. Two groups — milleporines and stylasterines — have a stony growth that fossilizes; they appeared in the Cretaceous and are widespread through the Cenozoic.

Hyenas see ***Pachycrocuta***.

Hyeniales an order of primitive shrubs with short, forked leaves in whorls, *incertae sedis* between sphenophytes and pteridophytes; global distribution, Devonian.

Hylaeosaurus armatus a species of ankylosaurian dinosaurs in the family Nodosauridae. One of the three species that Richard Owen assigned to his proposed order Dinosauria in 1842, it was squat and quadrupedal, 10–20 feet long, and probably well-armored. Europe, Early Cretaceous, 135 Ma.

Hylobatidae the gibbons, the lesser apes, classified with humans and the Cercopithecidae in the superfamily Hominoidea and infraorder Catarrhini. The family includes four extant genera: *Symphalangus* (the siamangs), *Hylobates, Nomastus*, and *Hoolock*. Although these genera appeared in a rapid radiation 5–7 Ma, only two extinct genera are known, ***Bunopithecus*** and ***Junzi***, *q.v.* Southeast Asia, late Miocene to Recent.

Hylonomus a monospecific genus of anapsid reptiles, placed tentatively in the Romeriida and family Protorothyrididae. The earliest-known unquestioned amniote, known from Nova Scotia about 312 Ma, *H. lyelli* was 9 inches long and had a long tail. Canada, Middle Pennsylvanian.

Hymenoptera an order of insects that includes bees, wasps, and ants; global distribution, Early Triassic to Recent.

Hyolitha "u-bone," a group of enigmatic Paleozoic animals, long considered probable mollusks but in 2017 shown to be lophophorates, related to brachiopods. Up to 1.5 inches long, they are similar in some ways to annelids, the segmented worms. They have conical calcareous shells with an operculum closure at the large end and two curved extensions called helens protruding, along with short feeding tentacles. The shell generally appears triangular or u-shaped when crushed flat. There are two orders, the Hyolithida and the problematic smaller group Orthothecida. Widespread in the Cambrian, their numbers declined through the Devonian, but a few persisted to the end of the Permian.

Hyopsodontidae a family of small, primitive ungulate mammals, possibly related to horses. Dachshund-like in appearance, they were generally insectivorous and herbivorous. They were unspecialized, having clawed toes and a generalized dentition. North and South America, Europe, Asia, and Africa; early Paleocene to Eocene.

Hypacrosaurus a duospecific genus of large hadrosaurid dinosaurs in the subfamily Lambeosaurinae. About 30 feet long and weighing almost 5 tons, it resembles *Corythosaurus* but has a higher and wider crest and very high neural spines, for which one species (from the Horseshoe Canyon Formation of Alberta) is named *H. altispinus*. The other species, *H. stebingeri* (from the Two Medicine Formation of Montana), is especially important for the discovery of a great number of hatchlings and embryos in eggs the size of a small soccer ball. Research on the embryos has indicated altriciality and shown, among other things, that their relatively long incubation time was almost 6 months, much longer than in birds. North America, Late Cretaceous, 84–67 Ma.

Hyperammina an elongate tubular foraminiferan in the suborder Textulariina; global distribution, Silurian to Recent.

Hypercalcified sponges sponges with nonspiculate, rigid calcareous basal skeletons, such as stromatoporoids, chaetitids, sclerosponges, chambered sphinctozoans, and archaeocyathans. These groups are important reef builders.

Hyperlioceras a genus of hildoceratid ammonoids in the family Graphoceratidae. Laterally compressed and involute, it first appeared at 171.6 Ma and marks the base of the Bajocian there. Europe and Saudi Arabia, Middle Jurassic, 171.6–168 Ma.

Hyperoartia a disputed class of lamprey-like vertebrates; synonym Petromyzontida. It includes principally the lampreys (the extant *Petromyzon* and its relatives) and dates back at least to the Devonian *Priscomyzon*; see also ***Tullimonstrum*** and ***Jamoytius***. Global distribution, Late Devonian to Recent.

Hypertragulidae a family of small artiodactyl ungulate mammals, among the earliest ruminants. Weighing only 5–9 pounds, they resembled very small deer. Europe, Asia, and North America; Eocene to Miocene.

Hyphalosaurus a genus of choristoderan reptiles in the family Hyphalosauridae. Very common in the Jehol Biota, it reached a length of almost 3 feet, with a very long neck and tail. Some specimens show skin impressions, and *Hyphalosaurus* may have been viviparous. China, Early Cretaceous, about 125 Ma.

Hyphantoceras a genus of heteromorph ammonitid ammonoids in the superfamily Turrilitaceae. It has a loose, helically coiled shell that stretches out to 4–5 inches long. Cosmopolitan, Late Cretaceous.

Hypochilus an extant genus of araneomorph spiders in the family Hypochilidae, the principal representative of the family. A basal araneomorph with primitive characters such as the cribellum and four book lungs, the modern lampshade spider *Hypochilus* seems to possess a mosaic of primitive and derived characters. Despite its presumably ancient origins, there are no definitive known fossil specimens. Found only in China and United States.

Hypseloconus a problematic genus of early Paleozoic gastropods. The uncoiled shell is high and conical, with an off-center apex. Although it was widespread and in some places common in the Cambrian and Ordovician, it is variously considered as belonging to the Monoplacophora, Brachiopoda, or a group of its own. Cosmopolitan, middle Cambrian to Middle Ordovician.

Hypsilophodon foxii a species of herbivorous ornithischian dinosaurs in the suborder Ornithopoda, the only generally accepted hypsilophodont. Known only from several specimens found on the Isle of Wight in the nineteenth century, *H. foxii* was 5–6 feet long and lightly built, weighing less than 50 pounds. It had a stiff tail, weak forelimbs with five long fingers on the manus, and four toes on the pedes. Its name refers to a frill along its spine, not to its dentition. England, Late Jurassic to Early Cretaceous.

Hypsilophodontidae a large, probably paraphyletic family of small ornithopod dinosaurs. From 3 to 6 feet long and lightly built, they were herbivorous and generally bipedal. Global distribution, Middle Jurassic to Late Cretaceous.

Hypsodont dentition high-crowned teeth with a flattened surface for chewing tough vegetation, with enamel extending the length of the tooth and past the gum line, and with cementum between the lophs of the tooth.

Hyrachyus a genus of ceratomorph mammals in the family Hyrachyidae. Known from hundreds of specimens, *Hyrachyus* was 4–5 feet long. Although generally considered to be related to the lophiodont tapirs, it has rhinoceros-like dentition. Holarctic distribution, Eocene.

Hyracodontidae a family of perissodactyl ungulates in the superfamily Rhinocerotoidea. Initially small and tapir-like, the later hyracodontids include the largest-known terrestrial mammals, the Indricotherinae (see ***Paraceratherium***). North America, Georgia, Kazakhstan, Pakistan, and China; early Eocene to early Miocene.

Hyracoidea an extant order of superficially rabbitlike mammals, related to modern sirenians and elephants. Widespread in Africa in the Eocene, the hyracoids ranged from cow-sized to mouse-sized. The order contains two families, the extinct Pliohyracidae and the modern Procaviidae. Africa, Europe, and Asia; Eocene to Recent.

Hyracotherium a genus of palaeotheres in the family Palaeotheriidae, generally considered the earliest-known perissodactyl and close to the ancestry of Equidae and brontotheres. Weighing up to 50 pounds, it had four toes on its forelimbs and three toes on its hindlimbs; its teeth were low-crowned. *Hyracotherium* had a global distribution in the early Eocene, as evidenced by whole fossil skeletons found in Europe and North America and partial skeletons elsewhere. See also ***Eohippus.*** Early to middle Eocene.

Hystricospherida an enigmatic group of spiky and spherical protist microfossils, one-celled marine algae. They are not well-known but are possibly related to the zygotes of freshwater chlorophytes or to dinoflagellates. Global distribution, Paleozoic to Recent.

I

Iapetognathus fluctivagus a species of denticulate conodont elements in the order Proconodontida and family Cordylodontidae. Its first appearance (currently considered to be 485.4 Ma) marks the GSSP for the beginning of the Early Ordovician in Newfoundland, Canada. The species is also known from the United States, Kazakhstan, and China.

Iberomesornis romerali a species of enantiornithean birds of the Early Cretaceous. Although known from only two partial specimens, it features several apomorphies of modern birds. It was the size of a sparrow and had a pygostyle, a short tail, and well-developed grasping claws on its feet, including a long hallux. See also **Enantiornithiformes**. Las Hoyas, Spain, Early Cretaceous, 126–125 Ma.

Ibyka a poorly known genus of early plants tentatively placed in the order Iridopteridales. It is considered a possible ancestor of horsetails. Middle to Late Devonian.

Icaronycteris a genus of early microchiropteran bats in the family Icaronycteridae. The earliest-known bat, it was about 6 inches long, had a wingspan of 15 inches, and probably used echolocation. The United States, Asia, and possibly Europe; early Eocene, 52.2 Ma.

ICBN International Code of Botanical Nomenclature. In 2011 the Eighteenth International Botanical Congress changed the name to *International Code of Nomenclature for algae, fungi, and plants*.

Icehouse conditions periods of extensive cooling on Earth, referring to periods of lower global temperatures and glaciation. They are associated with low levels of carbon dioxide, relatively calm volcanic eruptions, and low sea levels. The most recent, the Pleistocene glaciations, are well-documented, but the earlier cool peri-

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ods are not. The Karoo Ice Age was a period of cooling toward the end of the Carboniferous, extending into the early Permian; evidence for it has been found especially in Southern Africa and South America, but its extent and effects are not well-known. A cool period at the end of the Ordovician, roughly 450–420 Ma, is sometimes referred to as the Andean-Saharan Glaciation. Two longer periods of more severe cooling occurred in the Cryogenian Period, before the Ediacaran. Dated at 650–635 Ma, the Marinoan glaciation ended the Cryogenian after a warm span of about 25 million years. Marking the first part of the Cryogenian, the long Sturtian glaciation is dated between 717 and 660 Ma. Another long stretch of global cooling, probably the most severe but least understood, is called the Huronian glaciation, occurring between 2400 and 2100 Ma.

Ichnoentomology the study of insect trace fossils: the shape, walls, and fillings of traces left in soil, wood, leaves, and bones.

Ichnofacies temporally and geographically recurring trace fossil assemblages that provide information on the environment in which they occurred. There are vertebrate and invertebrate ichnofacies, the latter being especially important for the variety of information provided.

Ichnology see **paleoichnology**.

Ichthyodectidae "fish biters," a family of Mesozoic teleost actinopterygian fish in the extant superorder Osteoglossomorpha and extinct order Ichthyodectiformes. Most were between 3 and 16 feet long, some with large teeth. Global distribution, Late Jurassic to Late Cretaceous.

Ichthyolestes a genus of cetartiodactyl mammals in the family Pakicetidae. Fish-eating but mainly terrestrial, the fox-sized *Ichthyolestes* is closely related to the first whales. Pakistan, early to middle Eocene.

Ichthyopterygia a superorder or subclass of diapsid marine reptiles including ichthyosaurs and their smaller ancestors. Predatory and strong swimmers, they had a relatively short neck and porpoise-like body. Although basal ichthyopterygians were only 3 feet long, the later ichthyosaurs grew as long as 50 feet. Europe and Asia, Early Triassic to Late Cretaceous.

Ichthyornis dispar a species of ornithurine toothed birds in the order Ichthyornithiformes (the only recognized species of several described), known primarily from several specimens discovered in Kansas between 1870 and 2014. Similar to a small tern, it is closer to modern birds than are more archaic groups like the Enantiornithes. It is notable for its rows of sharp teeth, similar to those of mosasaurs, and for its vertebrae, which are fish-like, concave on both sides. Strongly keeled and muscular, *Ichthyornis* was probably a strong flyer. It seems to represent a transitional phase between dinosaur and bird, especially because both upper and

lower jaws were mobile, like that of modern birds, but its pincer-tip beak also had a powerful bite, with musculature like that of nonavian dinosaurs. North America, Late Cretaceous, 87–82 Ma.

Ichthyosauria an order of specialized diapsid marine reptiles in the superorder Ichthyopterygia, with an elongated snout and a fish-shaped body with four paddle-shaped limbs. They generally had a broad, twin-fluked tail, sometimes vertical, and some species had a dorsal fin. Ichthyosaurs were viviparous and ranged in length from 4 feet to more than 50 feet. They are notable for having larger eyes than any other vertebrate animal: the eyes of *Temnodontosaurus* and *Ophthalmosaurus* were 8–9 inches across. The ichthyosaurs declined in the Late Jurassic and Cretaceous, relative to the mosasaurs and plesiosaurs, and the latest is dated at 90 Ma. See also **Shonisaurus**. Global distribution, Early Triassic to Late Cretaceous.

Ichthyosaurus the type genus of the order Ichthyosauria. It grew to 8–10 feet long, much smaller than most ichthyosaurs. Europe and Asia, Late Triassic to Early Jurassic.

Ichthyostega a genus of primitive labyrinthodont amphibians in the clade Tetrapodomorpha, close to the early ancestry of all terrestrial vertebrates and among the first to adopt an amphibian habit. Its pedes had seven digits, but a fossil manus has not been found. The skull was broad and flattened, and some species attained lengths of 3 feet. See **Tetrapoda**; Greenland and Europe, Famennian Age, Late Devonian.

ICSN International Code of Stratigraphic Nomenclature, the generally accepted authority for the names assigned to rock strata.

Ictidosauria see **Tritheledontidae**.

ICZN International Code of Zoological Nomenclature, the generally accepted authority for animal nomenclature; the 4th edition was issued in 1999, and a 5th edition is planned for 2018.

Iguania an extant suborder of lacertilian squamates that includes iguanas, chameleons, and dragon lizards, the Agamidae. Iguanians are morphologically distinct in having a large, fleshy tongue and an acrodont dentition, but their evolutionary relationship to other lizards is highly disputed. The earliest-known iguanian is *Bharatagama rebbanensis*, known from one specimen from India, dated at about 190 Ma. See also ***Magnuviator, Afairiguana, Arretosaurus,*** and ***Anqingosaurus***. Global distribution, Early Jurassic to Recent.

Iguanodon a genus of bulky ornithischian dinosaurs in the suborder Ornithopoda, one of the first dinosaurs to be described. Named for its set of iguana-like teeth, the herbivorous *Iguanodon* was one of the largest animals of its time, from 30 to 40 feet

long and about 3 tons. Although basically quadrupedal, it could also maneuver bipedally. Richard Owen originated the concept of the Dinosauria as a separate group of reptilelike animals in 1842 on the basis of the ornithopod *Iguanodon*, the theropod *Megalosaurus,* and the nodosaurid *Hylaeosaurus*. The genus *Iguanodon* has seen many revisions and reassignments of species, and it is still the subject of debate. It was first described from English specimens in the 1820s and is known more fully from many complete skeletons of *Iguanodon bernissartensis*, found in a Belgian coal mine in the 1870s. Europe, the United States, and probably Asia and Africa; Early Cretaceous, 140–120 Ma.

Iguanodontia the clade of ornithischian dinosaurs based on *Iguanodon* and including *Parasaurolophus* and the other hadrosaurs, camptosaurs, and other herbivorous dinosaurs. They were generally large, bulky, and bipedal, with several species optionally quadrupedal. Most were basically three-toed, and several had a thumb spike. The earliest iguanodonts appeared in the Jurassic, but they flourished worldwide in the Early Cretaceous, and some lasted to the end of the Cretaceous.

Illaenus a genus of medium-sized isopygous trilobites in the order Corynexochida and family Illaenidae. *Illaenus* grew as large as 2 inches, its cephalon had a high profile, and it had two short and recurved genal spines. The Illaenidae persisted from the Early Ordovician to the late Silurian. Europe and North Africa, Middle Ordovician.

Impunctate see **punctate**.

Inadunata a class or subclass of stalked crinoids that recent research identifies as polyphyletic. The members of its three orders (Cladida, Disparida, and Hybocrinida) are being reassigned. Global distribution, Early Ordovician to Middle Triassic.

Inarticulate see **articulate.**

Incertae sedis "uncertain seat," of undefined classification.

Incisoscutum ritchiei see **Gogo Formation.**

Index fossil a morphologically distinctive fossil taxon that characterizes a particular time period or biozone, usually found in a limited number of strata. Index fossils are abundant and widespread but short-lived so that their presence in a stratum makes it possible to correlate widespread occurrences of the stratum. Also referred to as guide, indicator, marker, or zone fossil.

Indocetus a genus of archaeocete cetaceans in the family Protocetidae, one of the earliest aquatic whales. Its four sacral vertebrae are fused to each other and to its pelvis, so that it may have been able to support its weight on land. It probably used its hindlimbs rather than its tail in swimming. India, early Eocene.

Indohyus a genus of artiodactyl mammals in the family Raoellidae. *Indohyus* was deerlike in shape and about the size of a raccoon, but several distinctive features show that it may be closely related to whales; one was a thickened ear bone that improved underwater hearing, a character now found only in cetaceans. Some consider *Indohyus* a close relative of the Anthracotheriidae. Asia, middle Eocene.

Indricotherium see ***Paraceratherium***

Infaunal see **epifaunal.**

Inferior Oolite see **Great Oolite**.

Infulaster a genus of atelostomate sea urchins, irregular euechinoids in the order Holasteroida and family Holasteridae.

Europe, Late Cretaceous, 95–90 Ma.

***Infulaster-Hagenowia* lineage** an echinoid lineage of the Late Cretaceous displaying extreme evolutionary changes. Nut-shaped but with a noticeable apical peak, *Infulaster excentricus* probably gave rise to *Hagenowia rostrata* in the Coniacian (about 88 Ma), with an elongate rostrum and a decrease in size. The process continued with other species and ended with *H. blackmorei* in the Campanian (about 80 Ma), which was even smaller and had an even taller rostrum. Europe, Late Cretaceous.

Ingentia prima a species of early sauropodomorph dinosaurs in the family Lessemsauridae. Estimated at more than 30 feet long and up to 10 tons, *Ingentia* is among the largest early sauropodomorphs. It is known from several fragments, including the vertebrae, arm, and shoulder bones. San Juan Province, Western Argentina; Late Triassic, about 210 Ma.

Iniopterygiformes an unusual order of holocephalic fish in the class Chondrichthyes, distantly related to the modern Chimaeriformes, the ghost sharks. They ranged from 6 to 18 inches long and had a cartilaginous skeleton; a specimen from Kansas has a fossilized brain inside its intact skull. They are named "nape wing" for the distinctive pair of winglike fins high on their back. The United States, Late Devonian to Late Carboniferous.

Inkayacu paracasensis a species of large penguins that lived in Peru in the late Eocene. It was very similar to modern penguins except that it was about 5 feet tall, weighed about 120 pounds, and had a long beak. A specimen found in the Paracas National Reserve in Peru is also notable for having well-preserved feathers that may have been brown and gray.

Inoceramus a very large genus of cryptodontan bivalves in the order Praecardioida and family Inoceramidae. It was suboval, with a beak and prominent concentric

growth lines; some species were over 3 feet long. The inoceramids declined gradually for at least 10 million years before disappearing about 1.5 million years before the end of the Cretaceous. Global distribution, Early Jurassic to Late Cretaceous.

Insecta a class of arthropods in the subphylum Hexapoda; the largest class of animals, with almost a million named species. Insects' most basic apomorphies are a chitinous exoskeleton, six jointed legs, three segments in the thorax, and compound eyes. The only invertebrates that have achieved flight, most groups of insects have four wings presently or had them at an earlier stage of their evolution (see also **Pterygota**, **Diptera,** and **Coleoptera**). Insects first appeared in the Early Devonian, but their fossil record is very sparse through the Devonian and Carboniferous. The earliest-known insect is a springtail from the Devonian Rhynie Chert of Scotland (see **Rhyniognatha**), and the first definitive flying insects appeared in the Late Carboniferous (see **Ensifera**). The insects experienced a massive radiation in the Cretaceous along with the angiosperms.

Insectivora an abandoned name for a grouping of the many small mammals that became widespread in the Cretaceous, preying mainly on insects; see **Eulipotyphla**.

Invertebrate an informal term for all non-vertebrate metazoan animals.

Involute especially of ammonoids, tightly coiled, with successive whorls overlapping and often covering most of the surface of earlier ones.

Iridopteridales one of the widespread but enigmatic orders of early vascular plants called cladoxylopsids. The whole plant structure is unclear because its trunk and branch connections are not known. Global distribution, Middle to Late Devonian.

Isanosaurus a monospecific genus of sauropod saurischian dinosaurs. *I. attavipachi* is important as one of the earliest sauropods, but it is poorly known from fragments of one skeleton, dated at about 210 Ma. Thailand, Late Triassic.

Isastraea a genus of scleractinian corals in the family Montlivaltiidae. Its multirayed corallites are generally cerioid. Widespread in the Jurassic and Early Cretaceous, it may have been able to live in cooler water than most other reef-building corals. North America, Europe, and Africa; Late Triassic to Late Cretaceous.

Ischadites an enigmatic genus of benthic marine organisms currently classified as algae in the obscure family Receptaculitidae. Its globose body resembles a sponge, with spiral rows of interlocking plates. North America and Europe, Middle Ordovician to Early Devonian.

Ischigualasto Formation a rock formation in Northwestern Argentina, important especially for tetrapods of the Late Triassic, the best-known of which are the early

dinosaurs. See also ***Chromogisaurus, Eoraptor, Herrerasaurus, Panphagia,*** and ***Pisanosaurus***. Upper Triassic, mainly Carnian but extending into the Norian, 231–226 Ma.

Ischnacanthiformes an order of acanthodian fish. Slender, lightly armored nektic predators, they were the largest acanthodians, some species growing as long as 6 feet. Canada and Europe, restricted to Early Devonian.

Ischyromyidae a basal family of sciuromorph rodents. Known from France to North America through the Eocene, they gave rise to the Gliridae and other modern rodents. It is thought that they were scansorial and probably competed with early scansorial primates (see also **Paramyidae**). North America, Europe, and Asia; Paleocene to Oligocene.

Isectolophidae a family of perissodactyl ceratomorph mammals in the superfamily Tapiroidea. They probably descended, along with the Helaletidae, from *Homogalax*, an early Eocene tapiroid of Asia and North America, and are also related to the ancestral proto-horse *Hyracotherium*. North America, Europe, and Asia; early to late Eocene.

Isisaurus a genus of titanosaurian sauropodomorph dinosaurs. About 60 feet long and 20 feet high, *Isisaurus* had unusually long forelimbs and a thick, vertically directed neck, therefore probably a very high browser. India, Late Cretaceous, 71–69 Ma.

Island dwarfism a process resulting in reduced size in a population of animals isolated on islands from other populations of the same species; see ***Bubalus, Europasaurus,*** and ***Homo floresiensis***.

Island gigantism evolutionary increase in size of a species isolated on an island. A relatively uncommon occurrence compared to island dwarfism, island gigantism is nevertheless known in dozens of cases, notably *Deinogalerix* and *Harpagornis*.

Isocrinus a genus of articulate stalked crinoids in the order Isocrinida and small family Isocrinidae, similar to *Pentacrinites*. *Isocrinus* had long, branched arms and a 1-inch crown; its star-shaped stem was attached to the substrate by a horizontal cirriferous runner. Global distribution, Early Triassic to Miocene.

Isoptera the termites, a suborder of insects in the order **Blattodea**, *q.v.*

Isopygous of trilobites, having a cephalon and pygidium of approximately the same size.

Isorophusella a genus of small edrioasteroid echinoderms in the order Isophorida and family Agelacrinitidae. In size, shape, and habit, it was very similar to

***Carneyella**, q.v.* It differed in having its five ambulacra only slightly curved. Canada, Early Ordovician, 455 Ma.

Isotelus rex the largest-known trilobite, a species in the order Asaphida and family Asaphidae. With a smooth, subtriangular cephalon and pygidium, it is especially notable for its isopygous shape and its size: 28 inches long, 3 inches high, and 16 inches wide. Europe, North America, and Asia; Middle to Late Ordovician.

Itagnostus a genus of agnostid trilobites in the family Peronopsidae. It was isopygous, generally with a narrow thorax. Canada, Russia, Australia, and Antarctica; middle Cambrian.

Ixalerpeton a monospecific genus of dinosauromorph archosaurs in the family Lagerpetidae. About 2 feet long, *I. polesinensis* is represented by specimens of two individuals, one of them with a skull and forelimbs. It was found in 2014 alongside a specimen of a sauropodomorph dinosaur, *Buriolestes*, in the Santa Maria Formation of Southern Brazil and is dated between 237 and 234 Ma. Like some other basal dinosauromorphs, *Ixalerpeton* has characters associated with dinosaurs, including a crest-shaped fourth trochanter on the femur. Brazil, early Carnian of the Late Triassic.

Ixodida the ticks, an order of parasitiform arachnids, formerly called Metastigmata. The Ixodida are divided into two main families, the Ixodidae (hard ticks) and the Argasidae (soft ticks) and the smaller monotypic family Nuttalliellidae. Their fossil record is sparse, but the earliest specimens appear in the Cenomanian (100 Ma), and genetic researchers believe that ticks parasitized diapsids and therapsids at least as far back as the Permian. They have thrived along with browsing mammals since the spread of grasslands in the Eocene. North America and Asia, Late Cretaceous to Recent.

J

Jaekelopterus a genus of giant eurypterids in the family Pterygotidae. Estimated at 7–8 feet long but known only from partial remains, it may be the largest arthropod known. The type species is *J. rhenaniae* (Germany) and the other reported species is *J. howelli* (Wyoming). Germany and the United States, Early Devonian, 411–406 Ma.

Jamoytius kerwoodi an early lamprey-like jawless fish, long considered the earliest vertebrate; now tentatively placed in the disputed class Hyperoartia. About 10 inches long, it had lateral eyes, a terminal mouth, and scales. Although it has been considered an anaspid ostracoderm, its classification is still in dispute. Known only from Scotland, early Silurian, 443–422 Ma.

Janassa bituminosa the type species of the family Janassidae, poorly known cartilaginous fish in the family Petalodontidae, known primarily from teeth; the United States and Europe, Mississippian to Permian.

Janjucetus a genus of stem-mysticete whales in the family Mammalodontidae. About 11 feet long, it is notable for its short skull, its large eyes, and especially its large teeth. It had no baleen, a principal character of modern mysticetes. See also ***Llanocetus***. Australia, known only from one well-preserved specimen of the late Oligocene.

Java Man a set of fossil bones discovered at Trinil, Java, about 100 km from Ngandong, where the Solo Man remains were found. First classified as *Pithecanthropus* or a subgenus *Javanthropus*, it is now considered *Homo erectus*. See also **Jetis**. Indonesia, Pleistocene, about 1.5 million years ago.

Jebel Irhoud a cave site in Western Morocco where a hominin skull and body fragments were found in the late twentieth century. The remains were at first thought to be of Neanderthals, but analysis of the specimens in 2017 shows a non-prognathous

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face and other modern traits and estimates the date of the find at 300,000 years ago. If confirmed, this estimate would put the distribution of *Homo sapiens* throughout the continent 100,000 years earlier than previous estimates.

Jehol biota "hot river," a fossil community seen in several Konservat-Lagerstatten of Liaoning Province in China, found in the Lower Cretaceous Jiufotang and Yixian Formations, an area known for numerous hot springs. The species are dated between 133 and 110 Ma, the dates sometimes being uncertain because of problems dating the hundreds of fine-grained volcanic lacustrine deposits that have preserved very detailed structures in the fossils. The best-known fossils are dated between 130 and 120 Ma, in the Yixian Formation. The most striking are a range of feathered dinosaurs such as *Jeholornis, Microraptor*, and *Sinosauropteryx;* proto-birds such as *Confuciusornis*; and mammals (see ***Repenomamus*** and ***Eomaia***). Others are reptiles (see ***Hyphalosaurus***), insects, and some of the earliest angiosperms. See also ***Caudipteryx, Protarchaeopteryx, Beipiaosaurus***, and ***Sinornithosaurus***.

Jeholodens a small eutriconodont mammal in the proposed family Jeholodontidae. Known from one complete and articulated skeleton, it had large eyes and prehensile limbs and tail and was probably nocturnal and scansorial. China, Early Cretaceous, 125 Ma.

Jeholornis a genus of birdlike theropod dinosaurs. Like *Archaeopteryx* and other proto-birds, it is notable for its long, bony tail with feathers at the end rather than the pygostyle tail of modern birds. There are some traces of wing feathers as well. Omnivorous, eating insects and seeds of various plants, *Jeholornis* was about the size of a turkey, almost 3 feet long from beak to tail. The type species is *J. prima*, and other species with varying dentition, such as *J. palmapenis*, have been found. Hebei province, China; Early Cretaceous, about 120 Ma.

Jeholosaurus a monospecific genus of ornithischian dinosaurs in the family Thescelosauridae. Bipedal and probably herbivorous, *J. shanyuangensis* is known from two partial juvenile specimens from the Yixian Formation, dated about 125 Ma. China, Early Cretaceous.

Jetis fauna a Pleistocene assemblage in Java that contains fragmentary remains of *Homo erectus* along with sabertooth cats, a giant anteater, and several other mammals. See also **Ngandong** and **Trinil**. Indonesia, middle Pleistocene.

Jianfengia multisegmentalis a species of early arthropods known only from the Chengjiang biota. About half an inch long with many short legs and at least two anterior appendages, it is morphologically similar to *Opabinia*, of the Burgess Shale. China, early Cambrian, 530–515 Ma.

Jinzhousaurus yangi a species of ornithischian dinosaurs in the suborder Ornithopoda. Known from a complete skeleton, it was about 25 feet long and was

probably bipedal; it had small vertical scutes along its spine. *Jinzhousaurus* is tentatively considered a hadrosaurid on the basis of a spikelike thumb and a small crest at the top of its long, almost rectangular head. Yixian Formation, China, Early Cretaceous, 120 Ma.

Jiufotang Formation a Lower Cretaceous (Aptian) Lagerstätte in Liaoning Province; taxa from the formation are an important part of the Jehol biota. The formation has produced many feathered dinosaur specimens as well as pterosaurs, birds, turtles, frogs, insects, arachnids, and plants. Preservation of fine detail was possible especially because of fine volcanic ash deposits in a lacustrine environment. The Jiufotang Formation is underlain by the Yixian Formation and is dated at probably 121–119 Ma. China, Early Cretaceous.

Joannitidae a family of ceratitid ammonoids in the superfamily Arcestoidea, small and generally smooth-shelled. Eurasia and Alaska, Middle to Late Triassic, 235–206 Ma.

Joffrichthys a genus of freshwater fish in the superorder Osteoglossomorpha and family Osteoglossidae. A basal osteoglossomorph, it was 5–6 inches long and relatively deep-bodied. North America (Alberta and North Dakota), Paleocene.

Joggins Formation a Lower to Middle Pennsylvanian site in Nova Scotia whose strata record an area of swamps and periodically flooded forests. It is important especially for an early terrestrial vertebrate fauna, including the temnospondyl *Dendrerpeton* and the basal amniotes *Hylonomus* and *Paleothyris*. Canada, Late Carboniferous, 315 Ma.

John Day Fossil Beds a series of Eocene, Oligocene, and Miocene Konzentrat-Lagerstätten in Central Oregon. Several formations represent one of the most complete sequences of Cenozoic strata in the world, covering a period of more than 40 million years and including a great variety of animal and plant specimens. Some of the notable mammals from the three sites are the predatory feliforms *Nimravus, Dinaelurus*, *Patriofelis*, and *Pogonodon*; bison-sized entelodonts, such as *Archaeotherium* and *Daeodon*; the rhinoceros *Diceratherium*; the chalicothere *Moropus oregonensis*; the dwarf brontothere *Xylotitan*; the mouse deer *Hypertragulus*; and amynodonts. See also **Clarno Nut Beds** and **Painted Hills**. The United States, middle Eocene to late Miocene.

Josephoartigasia a genus of the largest-known rodents, in the family Dinomyidae. Related to the modern paca-rana, it is estimated between 1 and 2 tons and 10 feet long. Known only from a very large and almost complete skull, its size is uncertain but comparable to *Phoberomys*. Uruguay, Pliocene to early Pleistocene.

Jugulator a monospecific genus of eutriconodont mammals in the proposed family Volaticotheria. Slightly larger than *Volaticotherium*, *J. amplissimus* was probably

also a glider. It is known only from teeth and jaw fragments from the Cedar Mountain Formation in Utah. The United States, Cretaceous, 105–94 Ma.

Junzi imperialis possibly a new genus of gibbons in the family Hylobatidae. Discovered in a Chinese tomb dated at 2,300 years ago, it is known from distinctive cranial, mandibular, and dental remains and was given its binomial name in 2018.

Juramaia a genus of basal therian mammals known from an almost entire skeleton found in the Tiaojishan Formation. The type species, *J. sinensis*, is dated at 160 Ma and is important in determining the date when marsupials diverged from placental mammals. Yanliao biota, China, Late Jurassic.

Jurararaneus rasnitsyni a species of very small araneomorph spiders in the superfamily Araneoidea. Known from only one specimen, *Jurararaneus* is a cribellate araneoid, with a calamistrum of short leg bristles. Russia, Late Jurassic, 161–156 Ma.

Jurassic the second period of the Mesozoic Era, 201–146 Ma, divided into Early, Middle, and Late Epochs. As the supercontinent Pangaea continued to separate into northern and southern halves, more coastline appeared globally. The arid climate of the Triassic gave way to an almost "greenhouse" climate worldwide, with sea level rising and rain forests replacing deserts in many places. Gymnosperms diversified worldwide, and ferns, conifers, cycads, cycadeoids, and ginkgophytes all reached their maximum abundance.

The separating land masses were dominated by dinosaurs and pterosaurs, which had appeared in the Late Triassic. The stem mammaliaforms of the Late Triassic developed slowly at first but then diversified rapidly in the Middle Jurassic. Almost unnoticed, the first birds appeared near the end of the period. In the seas, plesiosaurs, ichthyosaurs, and sharks were dominant large predators, and the largest fish known (such as *Leedsichthys*) were among their prey. Marine invertebrates, especially ammonoids, also proliferated during the Jurassic.

Juravenator starki a species of very small coelurosaurian theropod dinosaurs, similar to the compsognathids. Known from a complete juvenile skeleton about 1.5 feet long, it is notable for some soft-tissue preservation, which indicates a unique combination of scaly skin and filamentous feathers. Germany, Late Jurassic, 156–151 Ma.

Juresania a genus of articulate strophomenate brachiopods in the order Productida and family Echinoconchidae. Its pedicle valve is strikingly domed, and the brachial is flattened, and both valves were lined with short spines. The United States, Europe, and Asia; Early Carboniferous to late Permian.

K

Kaiparowits Formation a sandstone and mudstone formation in Southern Utah, comprising layers dating between 76.6 and 74.5 Ma and overlying the Wahweap Formation. One of the most productive sites for plants and animals of the Campanian age, it has yielded crocodiles, turtles, and especially herbivorous horned dinosaurs such as *Kosmoceratops richardsoni* (found only here) and *Nasutoceratops titusi*; hadrosaurs, also herbivores, are common, as well as several other very large species. The tyrannosaurid *Teratophoneus curriei* is among the predators in the formation. Many of the specimens are complete, such as several whole dinosaur skeletons and a turtle that died with many eggs in her body. The United States, Late Cretaceous.

Kamoyapithecus hamiltoni an early species of apes, possibly the earliest catarrhine. Known from mandibular and dental fragments, it is dated at 24 Ma. See also ***Rukwapithecus***. Kenya, late Oligocene.

Kangaroo Island see **Emu Bay Shale**.

Kannemeyeriidae a family of very large dicynodont therapsids in the family Cryptodontidae. About 10 feet long, the family is generally taken to include *Placerias* and *Kannemeyeria* among others. North and South America, Asia, Southern Africa, and Russia; Early to Late Triassic.

Kaprosuchus saharicus a species of crocodiles in the family Mahajangasuchidae, variously estimated between 11 and 20 feet long. It is notable for three sets of large upper and lower tusks on each side of its jaws. These boar-like tusks worked like scissors to slice the flesh of prey, possibly dinosaurs. Niger, Early Cretaceous.

Karanisia a genus of lorisid primates found in 2002 in the Fayum Depression. The genus includes at least one undisputed species, *K. clarki*, which seems to have a toothcomb similar to modern lemurs. *Karanisia* represents the earliest evidence of anthropoid radiation. Egypt, middle Eocene, about 40 Ma.

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Karaurus sharovi "Karatau tail," an early species of salamanders in the family Karauridae. Known from one complete specimen found in the Karatau Mountains of Kazakhstan, *Karaurus* was about 7 inches long, with a very broad, frog-like head, a short body and tail, and sturdy legs. Kazakhstan, Late Jurassic, 155 Ma.

Karkenia the form genus of seeds associated with the Ginkgophyta; global distribution, Jurassic to Eocene.

Karoo Ice Age see **icehouse conditions.**

Karoo Supergroup an extensive series of formations spanning about 100 million years, important especially for the formations from the time between the Permian mass extinctions and the Early Triassic; South Africa, Late Carboniferous to Middle Jurassic.

Kayentachelys a genus of stem-turtles either in the order Testudines or in a more primitive classification of its own, found in the Kayenta Formation of Utah and Arizona. About a foot long, it possessed both a plastron and a carapace, and it seems to be a link between the primitive *Odontochelys* and modern turtles. The United States, Early Jurassic.

Kayentatherium a genus of Early Jurassic cynodont mammaliamorphs in the family Tritylodontidae, known from some anterior skeletal bones and several complete skulls found in Arizona; The United States, Early Jurassic.

Kazacharthra an order of freshwater branchiopod crustaceans in the family Ketmeniidae, possibly related to the Notostraca. Relatively large, up to 5 inches long, kazacharthrans had a large, heavy carapace and a flattened telson. Kazakhstan, Mongolia, China, and possibly Germany; Late Triassic to Early Jurassic.

Keichousaurus a genus of sauropterygian marine reptiles in the suborder Pachypleurosauria. Up to about 9 feet long, with a long neck and tail, *Keichousaurus* may have been viviparous. Guizhou Province, China; Early to Late Triassic, 249–236 Ma.

Keilor skull a skull found in 1940 in a late Pleistocene site in Southern Australia, classified as *Homo sapiens*. The skull, between 13,000 and 15,000 years old, led to the discovery of human habitation in the area about 31,000 years ago. The site is among the earliest locations of human habitation in Australia.

Kekenodon a poorly known genus of ancestral whales, placed tentatively in the Basilosauridae. New Zealand, Oligocene.

Kelenken the largest of the phorusrhacids, a monospecific genus of large flightless predatory birds. Between 7 and 10 feet tall and weighing up to 500 pounds, *K.*

guillermoi had the largest head of any known bird. Argentina, middle Miocene; see also ***Andalgalornis***.

Kellwasser event the extinction event that marks the boundary between the Frasnian and Famennian Ages near the end of the Devonian.

Kem Kem beds a site on the border of Algeria and Morocco. More than 100 miles long, the escarpment in Southeastern Morocco has produced many fossils from the middle of the Cretaceous, including several crocodylomorphs, pterosaurs, and turtles, and especially several large dinosaurs such as *Carcharodontosaurus* and *Spinosaurus*. Late Cretaceous, 100–94 Ma.

Kennalestes a genus of shrewlike eutherian mammals in the order Leptictida, known from several specimens found in Mongolia; China, Late Cretaceous, 75 Ma.

Kentrosaurus an African genus of ornithischian dinosaurs in the family Stegosauridae. About 15 feet long but weighing only 1 ton, the herbivorous *Kentrosaurus* was armored by several pairs of plates and spikes along the spine, as well as a large spike projecting from each shoulder. Tanzania, Late Jurassic.

Kenyanthropus platyops the name tentatively given to poorly known fossils, a skull, and fragments of a hominin found in the late 1990s by Meave Leakey; see also **Lomekwian industry**. Lake Turkana, Kenya, 3.5–3.3 Ma.

Kenyapithecus a middle Miocene hominoid primate, known from only a few East African fossils. Although similar to *Sivapithecus* and other Asian pithecines, *Kenyapithecus* is now thought more likely to be in the direct line of descent to the Hominidae. *Kenyapithecus* fossils date to around 16 million years ago, about 12 million years earlier than any presently recognized hominins, and the fossil record in between is incomplete.

Kepplerites a genus of ammonoids in the family Kosmoceratidae, about 5 inches in diameter with fine ribbing. Its first appearance marks the beginning of the Callovian Age of the Middle Jurassic at 166.1. Global distribution.

Keratin a fibrous protein, similar to chitin, that is an important protective material found in hooves, nails, skin, horns, feathers, beaks, claws, and whale baleen. It is also

the basic material of mammalian hair and is considered an important evolutionary contributor to the rise of mammals. Keratin has uncertain origins; a 2008 genetic study claims that keratin genes originated in an unknown reptile ancestor from about 300 Ma.

Kerygmachela a genus of enigmatic arthropod-like organisms tentatively placed in the family Anomalocarididae. Similar to the larger *Anomalocaris* in its spiny

anterior limbs and lateral lobes used in swimming, it is known only from the Sirius Passet deposits. Greenland, early Cambrian, 520 Ma.

Key bed a thin but widely occurring stratum of sedimentary rock composed primarily of a particular, easily identifiable material, sometimes of fossils. The prolific nautiloid *Orthoceras*, for example, forms key Ordovician beds in several places. The key bed most often referred to is the iridium layer that marks the end of the Mesozoic Era.

Kimberella an enigmatic genus of Ediacaran bilaterian organisms. It may be a primitive mollusk: benthic and sluglike, it is associated with scratches similar to those left by rasping polyplacophorans. Known from hundreds of oval specimens dated between 558 and 555 Ma, it ranged from less than an inch long to 6 inches. Australia and Eurasia, Ediacaran.

Kinorhyncha an extant phylum of microscopic (1 mm or less) marine invertebrates that live in soft substrates worldwide; called spiny-crowned worms. They are tentatively placed in the clade Scalidophora along with the Loricifera and the Priapulida. Kinorhynchs are marked by five or six rings of recurved spines around the head and by a segmented cuticle covering the body and spines that is molted often in early growth stages. Although they have almost no fossil record, they have been tentatively reported as phosphatized fossils from the early Cambrian, and they may be related to the similar but larger worms (1.5 inches long) described in detail in the Qingjiang biota. If they are thus related, kinorhynchs and loriciferans may represent a similar evolutionary process of miniaturization, appearing first in a macroscopic form but later only microscopically. Global distribution, early Cambrian to Recent.

Kirengellidae a family of early shelled organisms in the monoplacophoran order Tryblidiida. Their affinities are disputed, some researchers suggesting a possible brachiopod relationship. Middle Cambrian to Early Ordovician, 501–479 Ma.

Kirkbyella a genus of paleocopan marine ostracods in the superfamily Kirkbyoidea and family Kirkbyellidae. *Kirkbyella* is about 0.4 inches long and equivalved; its almost quadrilateral surface is pitted in a net-like pattern, and it has a dorsal sulcus. Holarctic distribution, Middle Ordovician to late Permian.

Kirkbyoidea a small superfamily of ostracods in the order Palaeocopida and suborder Kirkbyicopina. Reticulate and straight-hinged, they are found globally in the late Paleozoic, becoming extinct in the Triassic.

Kirkidium a genus of articulate brachiopods in the family Pentameridae. From 3 to 4 inches long, biconvex and astrophic, with a large pedicle valve. North America and Europe, Silurian.

Kirtland Formation an important sedimentary formation of the Late Cretaceous, located in the San Juan Basin of New Mexico and Colorado. It is known for many specimens of dinosaurs of the Campanian, including *Kritosaurus* and *Alamosaurus*, as well as many other vertebrates. The United States, 75–73 Ma.

Kloedenelloidea a large superfamily of ostracods in the suborder Kloedenellocopina; global distribution, Ordovician to Triassic but less abundant in the later Paleozoic.

Knightia a genus of clupeiform fish in the family Clupeidae. Generally from 4 to 8 inches long and herring-like, *Knightia* occurs in great numbers in the Green River Formation in Wyoming and is the most common fish fossil in shops around the world. North and South America, early Eocene.

Knightoconus antarcticus a species of monoplacophoran mollusks in the order Archinacelloidea. It had a chambered, conical shell and is a possible ancestor of the Cephalopoda. Known only from Antarctica, middle Cambrian.

Knorria a form genus of the bark of *Lepidodendron, Sigillaria*, and other Paleozoic trees.

Koilops herma a species of tetrapods described in 2016 as similar to *Greererpeton*; Scotland, Early Carboniferous (Tournaisian).

Kokartus honorarius a species of early salamanders in the family Karauridae; Kyrgyzstan, Middle Jurassic, about 167 Ma.

Kolponomos a genus of carnivorous mammals of uncertain classification but possibly a stem pinnipedimorph. Known from two specimens found on the Pacific Northwest Coast, it was bearlike in shape but had an unusual heterodont dentition. It had molars suited to crushing hard-shell mollusks and robust canines and strong jaw musculature similar to that of sabertooth cats. It is thought to have used its canines to pry mollusks loose from the hard substrate. The United States, middle Miocene.

Kolposaurus see ***Plotosaurus***.

Koolasuchus a genus of temnospondyl amphibians in the suborder Stereospondyli and family Chigutisauridae. One of the last temnospondyls, *Koolasuchus* is known from several fragmentary specimens. It is estimated to have been about 15 feet long, with a large, flat, triangular head. Australia, Late Cretaceous, 125–115 Ma.

Kootenayscolex barbarensis a species of proto-annelid worms. Known only from many specimens at the Marble Canyon site of the Burgess Shale, the segmented

body of *K. barbarensis* is covered with parapodia which bear tufts of chaetae, so that it looks like a modern bristle worm. But it also has bristles on its head and around its mouth, unlike any modern annelid. It is about an inch long, and the head also bears a pair of long palps and an antenna. Canada, middle Cambrian, 508 Ma.

Kosmoceras a large genus of ammonitid ammonoids in the superfamily Stephanoceratoidea. Most species are distinguished by a combination of ribs and tubercles. Global distribution in Callovian deposits, Middle Jurassic.

Kosmoceratops richardsoni a ceratopsian dinosaur in the subfamily Chasmosaurinae, notable for the 15 horns and spikes on its head and ornate neck frill. A herbivore about 15 feet long, it had a skull almost 6 feet long and seems to be closely related to a coeval Canadian chasmosaurine, *Vagaceratops irvinensis*. *Kosmoceratops* is known from only two specimens found in the Kaiparowits Formation of Southern Utah. The United States, Late Cretaceous, 75 Ma.

Kotlassia a genus of salamander-like seymouriamorphs in the family Kotlassiidae. About 3 feet long, it is known from skeletal fragments found near Kotlas, Russia. Late Permian.

Kritosaurus a genus of poorly known hadrosaurid ornithischian dinosaurs in the subfamily Saurolophinae. It was first found in the Kirtland Formation and is also known from fragments found in Montana, Alberta, and Mexico. North America, Late Cretaceous, 75–70 Ma.

Kronosaurus one of the largest pliosaurs, a genus of plesiosaurian reptiles in the family Pliosauridae. Up to 35 feet long, *Kronosaurus* had a short neck, four flippers, and a short tail. In a long, slender snout, it had conical teeth from 3 to 12 inches long; its prey included turtles and other marine reptiles. Australia and Colombia, Early Cretaceous, 120–100 Ma.

Kryptops "hidden face," a proposed monospecific genus of carnivorous saurischian dinosaurs in the clade Ceratosauria, known from fragmentary remains described in 2008. *Kryptops palaios* was about 20 feet long and is possibly one of the earliest abelisaurids. Some researchers believe, however, that it may be a chimera since some fragments were found 50 feet from others and may belong to a different dinosaur. Ténéré Desert, Niger, Early Cretaceous, 110 Ma.

K-T boundary see **Cretaceous extinction**.

Kuehneosauridae a family of gliding, lizard-like diapsid reptiles in the clade Eolacertilia, usually considered lepidosauromorphs. Lateral sails on either side of the body enabled them to glide but not fly. The type species *Kuehneosaurus latus*,

of the Late Triassic, was about 2 feet long with each sail about 6 inches wide, supported by a rib extending from the body. The United States and Europe, Early Triassic to Late Jurassic.

Kuehneotherium a genus of primitive shrew-sized mammals in the family Kuehneotheriidae, known from abundant tooth, dental, and mandible specimens but no complete skeletons. It had weaker jaws than the morganucodonts and probably subsisted on small insects and worms**.** Europe and Greenland, Late Triassic to Early Jurassic.

Kulindroplax perissokomos a species of mollusks in the class Aplacophora, the first unambiguous aplacophoran with chiton-like armor. A specimen found in England in 2012 connects for the first time the generally shell-less Aplacophora with the Polyplacophora (chitons); its underside has a fine covering of small spicules. Late Silurian.

Kumimanu biceae "Bice's monster bird," a species of very large penguins of the middle to late Paleocene. Known from several skeletal fragments discovered in 2017, it is estimated at almost 6 feet long and is dated surprisingly early for such a large penguin. As in the earlier *Waimanu*, its wings and beak are slightly longer than in later penguins, probably indicating a transition between their still-unknown flying ancestors and modern penguins. New Zealand, 59–56 Ma.

Kunmingella a genus of Cambrian crustaceans in the order Bradoriida. One of several crustaceans in the Chengjiang biota with a bivalved carapace over the head and abdomen. Known only from China, early Cambrian, 517 Ma.

Kutchicetus a monospecific genus of slender ancestral whales in the family Remingtonocetidae. *Kutchicetus minimus* was about 8 feet long and weighed between 200 and 400 pounds. Its four short, gracile limbs would give it only slight mobility on land, while its elongated and robust tail vertebrae indicate that it used caudal undulation for swimming, a transitional feature in the evolution of whales. It did not, however, have tail flukes. Pakistan and India, early Eocene.

Kutorginata a small class of primitive brachiopods, one of the four extinct classes in the subphylum Rhynchonelliformea; global distribution, early Cambrian to Early Ordovician.

Kutorginida the single order of brachiopods in the class Kutorginata. Its smooth, biconvex calcareous shells and primitive articulation show similarities to early Cambrian mollusks and hyoliths. Global distribution, early Cambrian.

L

La Brea Tar Pits a Konzentrat-Lagerstätte in Los Angeles that has produced many complete specimens of mammals and birds of the late Pleistocene. The bones are impregnated by asphalt, with little degradation of bone structure or proteins; very little soft tissue is preserved, however. More fossil birds have been produced here than anywhere else. The United States, dated between 38,000 and 11,000 years ago.

Labyrinthodonts a paraphyletic group of early amphibian-like tetrapods. Marked by conspicuous fangs and a labyrinthine infolding of the dentine, they descended from the rhipidistian fish and may be ancestral to all later amphibians. Global distribution, Early Devonian to Early Cretaceous.

Laccognathus a genus of lobe-finned sarcopterygian fish in the order Porolepiformes and family Holoptychiidae. It is named "pitted jaw" for three large fossae on the jaw, of unknown function. From 3 to 7 feet long, with a short, flattened head, *Laccognathus* was probably amphibious. Eastern Europe and Canada, Middle to Late Devonian.

Lacertilia the lizards, a suborder of lepidosaurian reptiles in the order Squamata. The Lacertilia are a paraphyletic group, with some genera being more closely related to the traditionally excluded suborder Serpentes than to other lizards. Groups usually included in Lacertilia are Lacertoidea, Gekkota, Scincomorpha, Anguimorpha, and Iguania. Lacertilians probably evolved in the Permian, but the oldest definitive specimens are from the Middle Triassic (see ***Megachirella***). They generally differ from snakes in having legs, external ear openings, and moveable eyelids. Global distribution, Triassic to Recent.

Lacertoidea an extant superfamily of lacertilian squamates. It is currently understood to include the enigmatic Amphisbaenia and the families Lacertidae, Teiidae, and Gymnophthalmidae. Global distribution, Paleocene to Recent.

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Laevicaudata see **Branchiopoda**.

Laganosuchus a genus of late Mesozoic crocodiles in the family Stomatosuchidae. About 20 feet long, it is especially notable for its flat, 3-foot-long head and snout. As in modern crocodiles, its short legs extending to the side kept it from moving easily on land. Niger, Cretaceous, 110 Ma.

Lagenida an order of benthic foraminiferans with finely perforate, monolamellar walls; global distribution, late Silurian to Recent.

Lagerpetidae a family of non-dinosauriform dinosauromorphs, especially significant for research in the basal dinosauromorphs; formerly Lagerpetonidae. It consists of three known genera: *Lagerpeton, Dromomeron,* and *Ixalerpeton*. The lagerpetids are all Late Triassic, ranging in age from the early Carnian to the late Norian. They were probably all bipedal and lightly built, with some features associated with dinosaurs. A dubious quadrupedal ichnogenus from an Early Triassic trackway in Poland (Olenekian, 251–247 Ma) is claimed to have several similarities to the Lagerpetidae. If confirmed, it would put the origins of dinosaur ancestry much earlier than currently thought. Argentina and the United States, 236–210 Ma.

Lagerpeton a monospecific genus of non-dinosauriform dinosauromorph archosaurs in the family Lagerpetidae. Known from fragmentary specimens, *L. chanarensis* is estimated at about 2.5 feet long and 10 pounds. Research in 2016 dated it at 236–234 Ma, similar to *Ixalerpeton* but earlier than other lagerpetids such as *Dromomeron.* Argentina, Late Triassic.

Lagerstätte a German mining term commonly used for a fossil location containing an exceptionally large number of specimens. Konzentrat-Lagerstätten produce many specimens which are not notably well-preserved but are important for their sheer numbers (such as nesting areas, bone beds, cave deposits, and coquinas). Konservat-Lagerstatten, on the other hand, are noted for quality rather than quantity, containing significant numbers of fossils preserved in exceptional detail, sometimes three-dimensional and sometimes retaining soft tissue and fragile appendages. Such exceptional preservation occurs under unusual conditions, such as certain combinations of chemical processes, an anoxic burial environment, or deposition in exceptionally fine sediment. Since they often preserve autochthonous groups of fossils, Konservat-Lagerstatten are especially useful in understanding the development and evolution of fossil ecosystems.

"Laggania" see ***Anomalocarididae***.

Lagomorpha an order of euarchontoglire mammals that includes hares, rabbits, and pikas; global distribution, late Paleocene to Recent.

Lagonomegopidae an enigmatic family of neocribellate spiders in the superfamily Palpimanoidea. Until 2019 known only from amber specimens, the family is now known also from two specimens found in the Jinju Formation of South Korea. These are notable especially for the crescentic light-reflective structures in their eyes, possibly an indication of nocturnal predation. Asia, Europe, and the United States; Early to Late Cretaceous, 113–85 Ma.

Lagosuchus talampayensis a species of small archosaurian reptiles of the Triassic, included with other lagosuchians in the Dinosauromorpha. Although it is incompletely known from only one partial specimen, it probably fits somewhere in the ancestral line leading to dinosaurs. Quadrupedal but optionally bipedal, it had an unreptilian hinged ankle joint that allowed it to walk erect with its legs under its body, a characteristic of dinosaurs. Argentina, Middle Triassic, 237–235 Ma.

Lambdotherium a contentious genus of perissodactyl mammals formerly placed in the Brontotheriidae but now considered only a close early relative. Although poorly known, it was smaller than the earliest accepted brontothere, *Eotitanops*. The United States and Canada, early Eocene.

Lambeosaurinae a subfamily of duck-billed ornithopod dinosaurs in the family Hadrosauridae. Ranging in length from 25 to 35 feet, the lambeosaurines are distinguished especially by a large, hollow cranial crest. *Lambeosaurus lambei* also had a backward-pointing spike behind the crest. They were herbivorous and could move both bipedally and quadrupedally. Other genera include *Corythosaurus, Hypacrosaurus*, *Olorotitan*, and *Parasaurolophus*. North America and Asia, Late Cretaceous, 86–66 Ma.

Lamella "plate," pl. lamellae; a platelike, layered process or organ of an organism.

Lamnidae an extant family of sharks in the order Lamniformes. The family includes the great white shark, *Carcharodon carcharias*, and its extinct larger ancestor *C. megalodon* (Miocene to Pleistocene). Global distribution, Cretaceous to Recent.

Lance Formation a Maastrichtian stratigraphic unit in western North America, coextensive in places with the Hell Creek Formation. Outcropping in Wyoming, Montana, and North Dakota, it contains an important group of dinosaurs and smaller vertebrates from between 69 and 66 Ma, just before the end-Cretaceous extinction.

Lancelets see **Cephalochordata.**

Land plants evidence of the earliest true land plants is found in fossilized spores from the Ordovician and in possible spores from the Cambrian. The earliest fossil plant specimens are known from the Silurian (see ***Cooksonia***).

Lantern see **Echinoidea**.

Laramidia the name given to the western part of North America that existed as a narrow island continent in the Late Cretaceous, when North America was split by tectonic activity and a rising water level of the oceans. The strata laid down in the resulting Western Interior Seaway are rich with Cretaceous fossils.

Las Hoyas Lagerstätte a site in Eastern Spain dated at 126–125 Ma in the late Barremian Age of the Early Cretaceous. Las Hoyas is well-known for the only known specimens of the enantiornithean birds *Eoalulavis* and *Iberomesornis*, important in establishing the development of flight in birds. The thin-bedded limestone strata, probably laid down in a freshwater environment, have also produced a great variety of fish, spiders, insects, and plants.

Latimeria an extant genus of lobe-finned fish in the order Coelacanthiformes and family Latimeriidae. The coelacanths were long considered extinct since the Cretaceous until the discovery of modern latimerians in the twentieth century. A specimen of *L. chalumnae* was discovered in 1938 near the Comoros Islands, and several others have been found along the East African coast since then; a second modern species of coelacanth, *L. menadoensis*, was discovered in Indonesia in 1997. The latimerians have fleshy lobe fins and may grow up to 6 feet long. Their fossil record is unclear, but some researchers believe they originated in the Triassic. See **Coelacanthidae** and **Tetrapoda**. Cosmopolitan, Triassic? to Recent.

Laugiidae a family of sarcopterygian fish in the subclass Actinistia, related to the modern coelacanths of *Latimeria*; Europe, Greenland, and China; Early Triassic to Late Jurassic.

Laurasia A term referring to the northern land masses that are now North America, Europe, and Northern Asia; Laurasia was the northern part of Pangaea. See **paleogeography** for dates**.**

Laurasiatheria a clade of placental mammals that appeared in Laurasia in the Cenomanian, at the beginning of the Late Cretaceous. It includes the carnivorans, ungulates, shrews, bats, whales, and pangolins; see also **Eutheria**. Cretaceous to Recent.

Laurentia the name given to the early North American land mass when it was a separate continent from the Cambrian to the Silurian.

La Voulte-sur-Rhône a marine Konservat-Lagerstatten of the Callovian that is notable especially for the number of soft-bodied cephalopods preserved by pyritization, such as *Dollocaris ingens*; see also ***Ophiopinna***. France, upper Middle Jurassic.

Law of the Unspecialized see **Unspecialized Descent.**

Lazarus taxon a taxon whose fossil record shows one or more significant gaps, with no morphological change between the first and last specimens.

Leaellynasaura amicagraphica "Leaellyn's lizard," a species of small herbivorous ornithischian dinosaurs in the order Ornithopoda. It was only 2 feet tall but 7 to 10 feet long with a very long tail. *Leaellynasaura* is known from two almost complete specimens found at Dinosaur Cove in Australia, which was close to the South Pole in the middle of the Cretaceous. It is notable for large optic lobes in its brain, which seem to represent a night vision adaptation. Australia, Early Cretaceous, 118–110 Ma.

Leancholia a genus of early arthropod-like organisms in the class Megacheira. Its body was 2 inches long, with an oval carapace and long antennae extending from two short anterior appendages. Known in the Burgess Shale and Chengjiang biotas. Canada and China, early to middle Cambrian.

Lebachia a genus of tall cone-bearing trees in the order Coniferales, of the late Paleozoic and possibly Mesozoic. Similar in appearance to the modern *Araucaria*, it is related to the earlier Cordaitaceae and may be ancestral to modern conifers. Global distribution, Late Pennsylvanian to Permian or Triassic.

Lectotype When the type of a taxon is identified by a set of syntypes, a single name-bearing specimen may at some point be designated as the lectotype, a later-selected holotype.

Leedsichthys problematicus a species of actinopterygian fish in the extinct family Pachycormidae. Possibly the largest fish known, this filter-feeding giant is estimated to have been more than 70 feet long. The pachycormids, however, have only partly calcified skeletons, making their fossils difficult to interpret. Europe and Chile, Middle Jurassic.

Leehermania see **Staphylinidae.**

Leioceras a genus of ammonitid ammonoids in the family Graphoceratidae. The type species, *L. opalinum*, is especially well-known from Dorset, England. Its first appearance marks the beginning of the Aalenian and Middle Jurassic at 174.1 Ma. The shell is 2–3 inches in diameter, involute, and smooth with sinuous ribbing. Europe and North America, 174 to 172 Ma.

Lejopyge laevigata a species of agnostid trilobites in the family Ptychagnostidae. Blind and isopygous, *L. laevigata* marks the beginning of the Guzhangian, the last age of the middle Cambrian, 501–497 Ma. Global distribution.

Lemdadella a genus of trilobites in the order Redlichiida, considered the earliest-known trilobite. Its cephalon is semicircular, with crescentic eye ridges, and its thorax is undivided. Europe, Africa, and Antarctica; early Cambrian, 521 Ma.

Lemuroidea an extant superfamily of strepsirrhine primates that includes at least the lemurs, and in some classification schemes the lorises and galagos also. Their origins are still disputed, but they probably arose from adapiforms or lorisoids in the Eocene. Africa, Eocene to Recent.

Lenticulina a large genus of foraminiferans in the family Nodosariidae. Global distribution, Permian to Miocene.

Leperditicopida a disputed order of ostracods, traditionally placed with the palaeocopids but now in the subclass Myodocopa. They are generally from 1 to 2 inches long, thick-shelled, and straight-backed. Global distribution, Ordovician to Permian.

Lepidocaris rhyniensis one of the earliest preserved freshwater crustaceans, the only species in the branchiopod order Lipostraca. Possibly related to the modern anostracan fairy shrimp, this small (0.12 inches) crustacean is the most common arthropod in the Rhynie Chert but is known only there, where it lived in ephemeral pools created by hot springs. Scotland, Middle Devonian.

Lepidocyclus a genus of rhynchonellid brachiopods in the family Rhynchotrematidae. Astrophic and inflated, with a subglobular shape, it had a herringbone pattern on its strong ribs and a strong fold in the brachial valve. North America, Asia, and Australia, flourishing from Middle to Late Ordovician and surviving into the early Silurian.

Lepidodendron "scale branch," a genus of treelike lycopodiophytes related to the club mosses, in the order Lepidodendrales. One of the most common fossils in the coal beds of the Pennsylvanian, it probably reached heights of 100 feet and diameters of about 4 feet, with narrow, grasslike leaves as long as 3 feet. The surface of the branches was a mat of closely spaced squares, and the branches ended in spore-producing cone structures that grew 1–3 inches in diameter and up to a foot in length. Global distribution, Early to Late Carboniferous.

Lepidophylloides a form genus of the leaves of *Lepidodendron*; Carboniferous.

Lepidoptera one of the largest orders of insects, it includes moths and butterflies. Its origins are obscure because of the lack of hard parts; the earliest definitively known are dated at 190 Ma (see ***Archaeopteris***), but wing scales resembling those of modern genera are dated at about 200 Ma. Europe, Early Jurassic.

Lepidosauria a large subclass of reptiles that includes the orders **Rhynchocephalia** and **Squamata**, *q.v.*

Lepidostrobus a form genus of the large cones (strobili) of ***Lepidodendron***, *q.v.*

Lepidotes a genus of semionotid actinopterygian fish. Generally about a foot long, some grew as long as 3 feet; they were covered with diamond-shaped ganoid scales and preyed on mollusks. Europe and South America, Early Jurassic to Early Cretaceous.

Lepospondyli a diverse subclass of small amphibian-like tetrapods. The lepospondyls include five orders: Adelospondyli, Aïstopoda, Lysorophia, Microsauria, and Nectridea. They are distinguished from the labyrinthodonts by spool-shaped centra in the vertebrae, the lack of fangs, and the lack of infolded dentine in the teeth. The group almost disappeared early in the Permian, with only one species surviving to the late Permian. Pennsylvanian to late Permian.

Leptaena a genus of articulate brachiopods in the order Strophomenida and family Rafinesquinidae. It grew up to 1.5 inches, with a convex pedicle and concave brachial valve. Its exterior is concentrically wrinkled and finely ribbed, with very irregular edges. Global distribution; Ordovician to Carboniferous.

Leptictida a possibly paraphyletic order of small eutherian mammals, possessing an unusual combination of primitive and specialized characters. One of the earliest branches from basal eutherians, they may be distantly related to the Euarchontoglires. North America, Europe, and Asia; Late Cretaceous to Oligocene.

Leptictidium "slender weasel," a genus of small mammals in the order Leptictida. It was 2–3 feet long from nose to tail but weighed only about 5 pounds. *Leptictidium* had a tail longer than the body; short, weak forelimbs; and strong, elongated hindlimbs that were adapted to running. Its cranium and dentition are archaic, and it was omnivorous. Among the few completely bipedal mammals besides humans, it used its tail for balance. Best-known from the Messel Shale Pit; Europe, early to late Eocene.

Leptochoeridae "slender pig," a family of early artiodactyl mammals in the superfamily Dichobunoidea, related to and possibly ancestral to the Entelodontidae; North America, middle Eocene to middle Oligocene.

Leptocleididae "slender clavicle," a family of small plesiosaurs in the clade Leptocleidia. Generally 8–10 feet long with a round body and short tail, they swam in shallow seas worldwide. Early Cretaceous, 140–115 Ma.

Leptocyon "slender dog," a genus of fox-like mammals in the family Canidae and subfamily Caninae, weighing about 7 pounds; North America, Oligocene through Miocene.

Leptodus a genus of articulate strophomenate brachiopods in the order Productida and family Lyttoniidae. *Leptodus* is characterized by an unusually thin and flattened brachial valve and an oyster-like pedicle valve that is cemented to the substrate or to other shells. Global distribution, Permian.

Leptograptid fauna an important fossil assemblage of the Ordovician that includes the slender planktic graptoloid *Leptograptus*, which became extinct at the end of the Ordovician; see **Graptolithina**.

Leptolepis "thin scale," a long-lived genus of actinopterygian fish in the family Leptolepidae. It was one of the earliest teleosts, with a skeleton made up completely of bone, as opposed to the combination of bone and cartilage in *Pholidophorus* and some other early teleosts. *Leptolepis* is named for its thin scales, which lacked the dentine or cosmine covering of most earlier fish. The combination of bony skeleton and thinner scales improved swimming ability. Global distribution, Middle Triassic to Early Cretaceous.

Leptomeryx a genus of primitive ungulate mammals in the family Leptomerycidae. One of the earliest cervids, it was a small deerlike ruminant, hornless, and weighing between 20 and 30 pounds. North America, late Eocene to early Miocene.

Lesothosaurus a monospecific genus of small, probably omnivorous ornithischian dinosaurs. About 7 feet long, with small forelimbs and manus, *L. diagnosticus* was evidently a fast runner. It is generally considered the only ornithischian outside the clade Genasauria. Lesotho, South Africa, Early Jurassic, 200–190 Ma.

Lessemsaurus a genus of early sauropodomorph dinosaurs, placed tentatively in the family Lessemsauridae with *Antetonitrus* and *Ingentia*. Known from vertebrae, a scapula, and limb bones, *Lessemsaurus* is estimated at 30 feet long, one of the largest early sauropodomorphs. The lessemsaurids seem to have differed from other sauropodomorphs in their pattern of growth, growing cyclically, in seasonal spurts. La Rioja Province, Western Argentina; Late Triassic, about 210 Ma.

Lewisuchus a genus of early archosaurian dinosauromorphs in the family Silesauridae; possibly synonymous with *Pseudolagosuchus.* Estimated at about 3 feet long and 4 pounds, it is known from several partial specimens. Argentina, Middle Triassic, 247 Ma.

Liangshanella a genus of bradoriid arthropods in the family Svealutidae. Abundant in the Burgess Shale biota and widely known in several other similar assemblages,

Liangshanella was oval and less than half an inch wide, with a bivalved carapace. Global distribution, early Cambrian to Early Ordovician, 516–478 Ma.

Liaoceratops yanzigouensis a species of early ceratopsian dinosaurs known only from two possibly juvenile horned skulls found in the Yixian Formation. Estimated to have weighed only 7 pounds, it is dated at 130 Ma and thought to be a basal neoceratopsian, near the time when the neoceratopsian branch of Ceratopsia diverged from the parrot-beaked Psittacosauridae. China, Early Cretaceous.

Liaoning see **Jiufotang Formation**.

Lias a term long used for a 20-million-year series of strata in Northwest Europe dated between the Rhaetian Age of the Triassic and the Toarcian of the Jurassic. The term also came to be used for that period of time, roughly the Early Jurassic. Modern dating revealed the inaccuracy of the references, and the term is now seldom used.

Libellulium a genus of flying insects in the order Odonata and superfamily Libelluloidea and placed variously in different families (e.g., Libellulidae, Petaluridae, Cymatophlebiidae). Distantly related to the modern dragonfly, it had a wingspan of 5–7 inches, and the hindwings were slightly broader and shorter than the forewings. North America and Europe, Jurassic.

Libelluloidea a superfamily of dragonflies, anisopteran insects in the order Odonata. They appeared in the Jurassic, were well-established at least in the Cretaceous, and have flourished worldwide since.

Librostoma a proposed subclass of trilobites, to include the orders Asaphida, Harpetida, Proetida, and Ptychopariida.

Lichida an order of spiny trilobites of the middle Paleozoic. The surface of the exoskeleton was grainy, even tubercular; some spines were long, but most were short and thick. The Lichida are sometimes grouped with the very spinose order Odontopleurida. Early Ordovician to Late Devonian.

Ligulalepis toombsi a new species of small, stem-osteichthyan fish, dated between 421 and 418 Ma, making it the oldest known osteichthyan. Known from two skulls and other remains, it had a blunt, rounded head At first labeled an actinopterygian, it is now thought to be a sister taxon to *Psarolepis* and ancestral to both actinopterygians and sarcopterygians. China, late Silurian.

Liliensternus a genus of Late Triassic theropod dinosaurs; possible synonym *Halticosaurus*. Known from several fragmentary specimens found in Germany and Switzerland, *Liliensternus* was a bipedal predator, about 17 feet long with strong hindlimbs and shorter forelimbs. In appearance it resembles an intermediate form

between the smaller *Coelophysis* and the larger *Dilophosaurus*. Europe, Late Triassic, 228–201 Ma.

Lilliput effect term given to the fact that, during extensive extinction events, species that survive the extinction are often significantly smaller than those of the period before the event. Some studies find that smaller and simpler organisms often survive more readily than larger and more complex ones. Others, such as on the therapsid *Moschorhinus*, indicate a dwarfing of the later individuals. The Lilliput effect is seen in some conodonts in the Kellwasser Event, and the much smaller average size of terrestrial animals after the end-Cretaceous extinction is an obvious example of decrease in size, but evidence for the causes is sparse. Foraminifera before and after that extinction seem to provide a good example of decrease both in size and in complexity.

Lima a genus of marine bivalves in the order Pectinida and family Limidae. Growing up to 3.5 inches long, *Lima* is commonly spinose, with protrusions along the margins that give it the name "file clam." It is equivalved, and the surface is radially ribbed and often rough. Global distribution, Late Carboniferous to Recent.

Limulus "looking sideways," one of two surviving genera of horseshoe crabs, chelicerates in the order Xiphosurida and family Limulidae. Horseshoe crabs are notable as an example of evolutionary stasis, the extant species being almost identical to their earliest-known ancestors. The genus *Tachypleus* is found on the coast of Asia, and *L. polyphemus* lives on the Atlantic Coast of North America. More closely related to spiders than to crabs, the Limulidae have survived since the Early Ordovician.

Limusaurus a monospecific genus of slender theropod dinosaurs in the family Noasauridae, closely related to *Elaphrosaurus*. Bipedal with short arms and about 6 feet long, *L. inextricabilis* is notable especially because hatchlings were born with several dozen teeth but lost them and did not replace them as they developed a beak. In the nineteen specimens known, adults were completely toothless, showing only traces of the tooth sockets. No other dinosaurs or reptiles are known to follow this pattern, although many replace and increase the number of their teeth as they grow older. The pattern is known, however, in the platypus and some fish. China, Late Jurassic about 160 Ma.

Linguatula serrata an extremely simplified pentastome, among the early Paleozoic specimens of this tongue worm, which is common today as a dog parasite. It is roughly cone-shaped, with the mouth and attachment hooks at the large end. Phosphatized specimens were found in the upper Cambrian strata of the Orsten Lagerstätten. Sweden, late Cambrian.

Lingula a well-known genus of marine intertidal brachiopods in the order Lingulida. About 2 inches long, with a 6-inch pedicle, *Lingula* has existed worldwide and essentially unchanged in shape since the middle Cambrian.

Lingulata an extant class of brachiopods in the subphylum Linguliformea. It includes three orders: Acrotretida, Lingulida, and Siphonotretida.

Lingulella a genus of inarticulate brachiopods in the order Lingulida and family Obolidae. Its many species are generally characterized by a long pedicle and a phosphatic shell. Global distribution, early Cambrian to Early Devonian, 516–409 Ma.

Lingulella waptaensis a well-known species of the widespread brachiopod *Lingulella*. It is prominent in the Burgess Shale biota and is especially notable for its long and thin pedicle stalk. Canada, middle Cambrian, 508 Ma.

Lingulida an extant order of inarticulate brachiopods in the class Lingulata. The most conservative of brachiopod orders, lingulids burrow in sediment, attached by a long pedicle. They are generally characterized by an oval, biconvex shape and a shell of calcium phosphate. Middle Cambrian to Recent.

Linguliformea a subphylum of inarticulate brachiopods, replacing the former class Inarticulata. The principal group of brachiopods in the Cambrian, it includes two classes: the extant Lingulata and the extinct Paterinata (early Cambrian to Ordovician). The Linguliformea differ from other brachiopods by having generally a dark, shiny organophosphatic shell, usually subcircular or conical. Global distribution, early Cambrian to Recent.

Lingulina a genus of generally tongue-shaped foraminiferans in the family Nodosariidae; Permian to Miocene.

Linoproductus a genus of articulate strophomenate brachiopods in the order Productida and family Linoproductidae. Subcircular in outline, it was about an inch in diameter with some spines and noticeable, sinuous ribs. The pedicle valve is very long and strongly beaked. Global distribution, Early Carboniferous to late Permian.

Linthia an early genus of atelostomate heart urchins in the order Spatangoida and family Schizasteridae. See also ***Schizaster***. North and South America, Europe, Asia, and North Africa; Late Cretaceous to Miocene, 94–12 Ma.

Liopleurodon a genus of large but short-necked marine plesiosaurs in the family Pliosauridae. *L. ferox*, the largest species, probably weighed between 1 and 2 tons and grew to about 20 feet long, although some estimates are much higher. The predatory *Liopleurodon* was an especially strong swimmer. Europe, Middle to Late Jurassic.

Lipostraca a monospecific order of freshwater branchiopods in the subclass Phyllopoda, containing the fairy shrimp *Lepidocaris rhyniensis*; known only from the Rhynie Chert of the Early Devonian.

Liriodendron an extant genus of trees in the family Magnoliaceae, known globally from the Cretaceous through the Eocene. Its range shrank during several late Cenozoic glaciations. It is also known in the form genus of the leaf, *Liriophyllum*. Middle Cretaceous to Recent.

Lisowicia bojani a species of large dicynodont synapsids in the family Stahleckeriidae. Although dicynodonts are well known from Africa, Asia, and the Americas, *Lisowicia* was the first significant European dicynodont, known from partial remains of several individuals and described in 2019. Estimated at 15 feet long and 9 tons, *Lisowicia* may have been the largest non-dinosaurian terrestrial tetrapod of the Triassic. It had a typical dicynodont snout with two tusks and a beak adapted for chewing tough vegetation. Dated near the Norian-Rhaetian line, *Lisowicia* is also the latest-known definitive dicynodont. Poland, Late Triassic, 212–205 Ma.

Lissamphibia a subclass of amphibians that includes all living members of the class: frogs, toads, salamanders, and caecilians. The fossil record is sparse for this group, but they are generally considered to have descended from one of the many Temnospondyli. See, for example, **dissorophidae**. Early Triassic to Recent.

Lithistida an extant polyphyletic group of demosponges whose massive skeleton of fused siliceous spicules is often preserved; global distribution, Cambrian to Recent.

Lithornithiformes an extinct order of flying birds in the extant infraclass Palaeognathae; North America and Germany, Paleocene to late Eocene.

Lithostrotion a genus of colonial rugose corals in the order Stauriida and family Lithostrotionidae, especially important in North American biostratigraphy of the Early Carboniferous. Its cerioid, cylindrical corallites grew up to half an inch wide with strong septa. Colony expanded horizontally by the addition of new vertical corallites. Global distribution, Early Carboniferous to Permian.

Litopterna an order of superficially horselike South American ungulate mammals in the superorder Meridiungulata, possibly descended from condylarths. Widespread from the Paleocene to the Pliocene and present in South America in the late Pliocene when true horses first appeared there. One family of litopterns, the Macraucheniidae, survived into the Pleistocene. South America, Paleocene to Pleistocene.

"Little Foot" a nickname for a possible species of australopithecine hominins found in South Africa and dated near 3.7 Ma. The disarticulated skeleton is estimated to be 90 percent complete and may be closely related to *Au. africanus*.

Littorina littorea the common periwinkle, an extant species of gastropods in the superfamily Littorinoidea and family Littorinidae. Widespread from Northern Europe to Siberia since the Paleocene, it is known in North America only in the last 200 years. Paleocene to Recent.

Littorinoidea a superfamily of gastropods previously placed in the discarded order Mesogastropoda but now considered simply part of the very large clade Caenogastropoda; Eocene to Recent.

Livyatan a genus of odontocete whales in the superfamily Physeteroidea. *Livyatan melvillei* is known from a middle-Miocene skull and mandible discovered in the Pisco Formation of Peru in 2010. A powerful predator, it had some teeth more than a foot long, longer than in any other animal known. It was about the size of a sperm whale, and its skull may have in fact contained a reservoir of spermaceti. A tooth found in Australia in 2016 and dated at 5–6 Ma is thought to belong to the genus. Miocene to Pliocene.

Lizard-hipped dinosaur a general term referring to saurischian dinosaurs.

Llanocetus denticrenatus a species of toothed stem-mysticete whales. Known only from an almost complete skull, it is estimated to have been around 25 feet long. Along with the Mammalodontidae and Aetiocetidae, it is an example of the transition from toothed terrestrial ancestors to the modern mysticetes, which are edentulous and equipped with baleen. Antarctica, late Eocene, 37–34 Ma.

Lobe-fins see **Sarcopterygii**.

Lobopod name given to a group of early, wormlike arthropods including *Aysheaia, Hallucigenia*, and possibly *Xenusion*. Cosmopolitan, early Cambrian to early Pennsylvanian.

Lomekwian industry the name given to a group of primitive tools found in Kenya near Lake Turkana. Dated about 3.3 Ma, they were evidently made by ancestors of the species *Homo*, such as Australopithecines or the uncertainly identified *Kenyanthropus platyops*.

London Clay a lower Eocene formation in Southern England. It has produced a large and diverse fauna and flora that indicate a tropical to subtropical climate in the early Eocene. Younger strata in the area, through the Eocene into the Oligocene, clearly show a cooling of the climate.

Longisquama "long scales," a monospecific genus of small four-legged reptiles. It bore long shafts, possibly feathered, on both sides of its body. Since it lived around 225 Ma, shortly after the appearance of the earliest dinosaurs, it may be evidence that birds did not descend from dinosaurs. The shafts of *L. insignis* (tentatively called "non-avian feathers") may not actually be feathers, and whether *Longisquama* is related to birds is unknown. It is not a dinosaur, but it does have a wishbone identical to *Archaeopteryx* (150 Ma) and similar to that of modern birds. Nevertheless, most authorities believe it is probably an ambiguous diapsid with no bearing on the origin of birds. Madygen Formation, Kyrgyzstan, Middle to Late Triassic.

Lonsdaleia a genus of colonial rugose corals in the order Stauriida, suborder Columnariina, and family Axophyllidae. It was cerioid or phaceloid, distinguished by the cerioid structure of the corallum and the star-burst shape of the individual polyps. The phaceloid species *L. duplicata* was widespread at the end of the Early Carboniferous. Asia, Europe, and North America; Late Devonian to Permian.

Lophialetidae a family of ceratomorph perissodactyl mammals in the superfamily Tapiroidea, widespread in Asia in the Eocene and Miocene. The manus is tridactyl, as in the other Asian family, the Deperetellidae.

Lophiodontidae a European family of perissodactyl ceratomorph mammals in the superfamily Tapiroidea. See also ***Hyrachyus***. Early to late Eocene.

Lophodont "crested tooth," having molar teeth with a hard chewing surface formed by transverse, triangular, or ring-shaped ridges, common in herbivorous mammals such as elephants, manatees, and tapirs.

Lophogastrida an extant and widespread order of nektic malacostracan crustaceans. Research in 2016 identified the earliest-known species, *Yunnanocopia grandis* and *Y. longicauda*, as part of the marine faunal radiation that followed the end-Permian extinction. China, Middle Triassic.

Lophophorates a large group of aquatic animals that feed by means of a lophophore, including brachiopods, bryozoans, phoronids, and hyoliths. Each is considered a phylum or class, but their exact relationships are debatable.

Lophophore a coil-shaped, feathery feeding structure in lophophorates, varying greatly in shape and length. Cilia on the lophophore sweep and pump food particles into the mouth of the animal.

Lorica see **Loricifera**.

Loricifera a poorly known extant phylum of protozoan animals, **w**ith only four dozen described species in the clade Scalidophora. Although they are only about 0.25 mm long, they are complex organisms, consisting of 10,000 cells. Similar to

the Priapulida but essentially microscopic, loriciferans live without light or oxygen, between particles of sediments, worldwide and in shallow or deep water. Somewhat mobile, they are protected by a body covering called a lorica, which contains complex organs including a brain and a digestive and excretory system. Although their fossil record is sparse, they seem to represent an example of evolutionary miniaturization. They may be related to the larger ***Sirilorica*** and ***Eolorica***, *q.v.* See also **Kinorhyncha**. Cambrian to Recent.

Lorisoidea an extant superfamily of strepsirrhine primates, related to the Lemuroidea. It contains the Galagidae and Lorisidae; the aye-aye (*Daubentonia*) is sometimes also included. Africa and Asia, Eocene to Recent.

Lovenechinus a genus of regular marine echinoids in the family Palaechinidae. Spherical in shape and up to 4 inches wide, *Lovenechinus* had straight and narrow ambulacra; its lantern and spines are unknown. The United States and Europe, Early Carboniferous.

Loxonema a genus of orthogastropods in the order Murchisoniina and superfamily Loxonematoidea. *Loxonema* is characterized by slender, high-spired shells with fine axial ornamentation lines. Global distribution, Ordovician to Middle Jurassic.

LUCA acronym for "last universal common ancestor," an unidentified type of prokaryotic organism thought to have been living almost 4 billion years ago, only half a billion years after the formation of Earth. It was presumably simpler than its offspring, probably single-celled with no distinct nucleus. The earliest definitive organic fossil is dated at 3.7 billion years ago. See also **Archaea**.

Luciferidae an extant family of decapod shrimps in the superfamily Sergestoidea. Until the 2018 discovery of an Early Cretaceous genus in the Araripe Basin, *Sume marcosi*, the family was known in the fossil record only from a late Pleistocene fossil from Australia. Cosmopolitan, Early Cretaceous to Recent.

Lufengosaurus a genus of sauropodomorph dinosaurs in the family Massospondylidae. Probably bipedal, 20–30 feet long, and almost 2 tons, *Lufengosaurus* is notable for the preservation of collagen in some embryonic bones, by far the earliest-known example of soft-tissue preservation in a fossil. Since the proteins in collagen vary from species to species, "collagen fingerprinting" may be important in phylogenetic research. The bones from at least 20 individual embryos show that the embryos were growing faster than in other dinosaurs. China, Early Jurassic, 197–190 Ma.

Lunataspis aurora a species of chelicerates discovered in Manitoba in 2008, the earliest-known xiphosuran. *Lunataspis* seems very similar to modern horseshoe crabs. Canada, Late Ordovician, 445 Ma.

Luoping biota a well-preserved assemblage of marine organisms from the Middle Triassic. Dated between 243 and 240 Ma, it represents the recovery of life forms following the end-Permian extinction. Significant fossils include a complete skeleton of the 7-foot ichthyosaur *Mixosaurus*, several nothosaurs, and many arthropods. China, Middle Triassic.

Lutreola see ***Neovison***.

Lutrinae the otters, a large subfamily of small mammals in the family Mustelidae. Partly aquatic, they occupy a wide range of terrestrial and marginal marine ecological niches. See also ***Enhydra***, **Pantolestidae,** ***Puijila***, ***Teruelictis***. Global distribution, early Miocene to Recent.

Lycaenodon "wolf tooth," a genus of small therapsids in the suborder Biarmosuchia, known from skulls found in the Karoo Basin of South Africa; late Permian, 259–254 Ma.

Lycaenops a genus of small therapsids in the family Gorgonopsidae. Only 2–3 feet long, *Lycaenops* had an erect posture and a formidable set of teeth. Middle to late Permian, 270–251 Ma.

Lycochampsa/Lycognathus see ***Cynognathus***.

Lycopodiophyta the lycophytes, the oldest division of vascular plants, known mainly for the large trees of the Devonian and Carboniferous but represented today by numerous families of smaller plants such as club mosses. Characterized by primitive, narrow leaves known as microphylls, they reproduce by shedding spores. Global distribution, middle Silurian to Recent.

Lycoptera a genus of small freshwater teleost fish in the extant superorder Osteoglossomorpha. One of the earliest-known osteoglossomorphs, it includes species that are index fossils for the end of the Jurassic and the Cretaceous in China; the genus is especially well-known in the Jehol biota. China, Mongolia, Korea, and Siberia; Late Jurassic to Early Cretaceous.

Lyginopteris a genus of early seed ferns in the division Pteridospermatophyta and order Lyginopteridales. Like many other Paleozoic plant names, *Lyginopteris* was originally the name of a form genus (in this case for the stem) but is used now for the whole plant. Small club-shaped glands occur on the surface of all parts of the plant. The United States and Europe, Late Devonian to Late Carboniferous.

Lyginopteridales an order of climbing seed ferns in the division Pteridospermatophyta. The earliest pteridospermatophytes, they were superficially very similar in appearance to true ferns. North America and Europe, Early Devonian to Carboniferous.

Lysorophia an order of snakelike amphibians in the extinct class Lepospondyli. They were tetrapods with a slender, elongate body with very small limbs, closely related to the Microsauria. The United States and Europe, Pennsylvanian to middle Permian.

Lystrosaurus a genus of dicynodont therapsids. A disaster taxon, it survived the end-Permian extinction and became the most common large terrestrial animal of the Early Triassic. Mammal-like and about the size of a large pig, *Lystrosaurus* was herbivorous and semi-aquatic, with only two large (canine) teeth. Its several species ranged in size from 2 to 8 feet long, and they probably used their robust forelimbs for digging and burrowing. Since its distribution encompassed Antarctica, Southern Africa, India, and China in the Early Triassic, it is one of the larger animals that provide information about the time of separation of Gondwana into its now widely removed parts. Late Permian to Early Triassic.

Lythronax argestes a species of theropod dinosaurs in the family Tyrannosauridae, known from one fairly complete skeleton discovered in the Wahweap Formation of Utah. Growing up to 25 feet long and 5,500 pounds, *Lythronax* is the earliest-known true tyrannosaurid and may be ancestral to *Tyrannosaurus rex*. The United States, Late Cretaceous, 81–80 Ma.

Lytoceras a genus of ammonitid ammonoids, the type genus of the family Lytoceratidae. It was 3–5 inches in diameter and had a smooth shell and a complex suture. Global distribution, Early Jurassic to Early Cretaceous.

Lytoceratida a conservative suborder of ammonoids in the order Ammonitida. Notable for having fewer but longer-lived species than other ammonoids, the early Lytoceratida evolved from phylloceratids and diversified into 12 families, the dominant one being the Lytoceratidae. Global distribution, Late Triassic to Late Cretaceous.

M

Machairoceratops "saber-horned-face," a monospecific genus of ceratopsid dinosaurs in the subfamily Centrosaurinae. Known from a partial skull described in 2016, it is estimated to be a medium-sized ceratopsian about 15 feet long. Like its cousin *Nasutoceratops*, *M. cronusi* was marked by two curved supratemporal horns, and it also had two unusual, forward-curving frill horns. Utah, the United States; Late Cretaceous, 82–80 Ma.

Machairodontinae "sabertooth," an extinct subfamily of cats with varying lengths of the canine teeth. The family is named for *Machairodus* and includes *Megantereon* and the later *Homotherium* and *Smilodon*. North and South America, Europe, Asia, and Africa; early Miocene to 10,000 years ago.

Machairodus a genus of lion-sized cats in the subfamily Machairodontinae; North America, Europe, Central Asia, and Africa; late Miocene to late Pleistocene.

Mackenzia costalis an obscure species of elongated, bag-like animals of the Cambrian. *Incertae sedis* was thought first to be an echinoderm and is now considered by some an early sea anemone, a cnidarian in the order Actiniaria. Known only from the Burgess Shale, Canada, middle Cambrian, 508 Ma.

Macluritidae an enigmatic family of early gastropod-like mollusks in the order Euomphalina, long placed in the now-abandoned Archaeogastropoda but now tentatively placed in a new order, Paragastropoda. Flattened, 2–4 inches wide, and hyperstrophically coiled, they were widespread in the Ordovician, but their classification has long been a source of contention. The type genus is *Maclurites*. Global distribution, Early to Late Ordovician.

Macoma an extant and very large genus of deep-burrowing clams in the order Cardiida and family Tellinidae. Often found in brackish-water environments, it includes several stenohaline species such as *M. balthica*. The earliest *Macoma*

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fossils appeared in the late Paleocene, and by the Miocene the genus had reached global distribution.

Macraucheniidae a family of perissodactyl ungulates in the order Litopterna, found only in South America. The Macraucheniidae appeared in the Eocene and were the last surviving litopterns, disappearing about 12,000 years ago. Research in 2014 *seems to show that Macrauchenia patachonica, although it looked like a camel, was most closely related to perissodactyls such as the horse, rhinoceros, and tapir*. South America, Eocene to Pleistocene.

Macrocephalites a genus of large ammonitid ammonoids **in the** superfamily Stephanoceratoidea. From 3 to 4 inches in diameter, it was involute and subglobose. Middle to Late Jurassic, Callovian, 166–155 Ma.

Macrofossil a fossil large enough to be studied directly without a microscope.

Macropodidae an extant family of marsupials in the order Diprotodontia. The Macropodidae include kangaroos and other extant genera as well as several extinct genera. Meganesia, late Oligocene to Recent.

Macroscelidea an order of eutherian mammals consisting of one family, the Macroscelididae. Although often called elephant shrews because of a very long snout and shrewlike shape, they are not closely related to either elephants or shrews. They are insectivorous, ranging from mouse-sized to rabbit-sized, and their very long hind limbs are adapted for jumping. Among the oldest extinct genera are *Herodotius* and *Metoldobotes*, known from the Oligocene beds of the Fayum Depression of Egypt. *Myohyrax* may be the oldest in the order, from a possible Eocene site in Namibia; and the more rodent-like *Mylomygale* is known from the Pliocene. The extant elephant shrews are not numerous but are widespread across Southern Africa, with one still present in North Africa. Early Oligocene to Recent.

Macrotaeniopteris a genus of low-growing plants with long, lanceolate leaves; global distribution, Early Triassic to Late Jurassic

Madygen Formation a Triassic Konservat-Lagerstatten in Central Asia, dated between 230 and 225 Ma. Its strata were laid down in forested floodplains with lakes, rivers, and swamps. Especially important because of the paucity elsewhere of Triassic insect fossils, it is known for its well-preserved insects and flora. Up to 90% of all insects known from the Late Triassic are represented here. Its most famous vertebrates are the single specimen of the unusual gliding reptile *Sharovipteryx* and several specimens of the enigmatic reptile *Longisquama*. Kyrgyzstan, Late Triassic.

Maevarano Formation a Maastrichtian site in Madagascar where reptiles, the large frog *Beelzebufo*, birds, mammals, and dozens of species of dinosaurs (includ-

ing *Majungasaurus*, *Masiakasaurus*, *and Rapetosaurus*) have been found. Two enigmatic birdlike specimens, *Rahonavis* and *Vorona*, are thought by some to have been capable of flight. Several bone beds in successive strata have been explored. Recent studies point to toxic algae as a possible cause of death of at least one group of different animals nestled together. Northwestern Madagascar, Late Cretaceous, 70–66 Ma.

Magnuviator ovimonsensis a species of iguanomorph lizards in the order Squamata. About 9 inches long and possibly insectivorous and herbivorous, it seems to be related to a family of Asian iguanians, the Temujiniidae. The United States, Late Cretaceous, 76 Ma.

Maiabalaena nesbittae a species of whales placed in the clade Chaeomysticeti, which consists of early mysticetes with neither teeth nor baleen. A basal mysticete, *Maiabalaena*, is known from an almost complete cranium and skeletal fragments. Along with the earlier discovery of the toothless species *Sitsqwayk cornishorum* (28–26 Ma), it bolsters the hypothesis that early baleen whales first lost their teeth and were suction-feeders for some time, developing baleen later. Oregon, the United States, early Oligocene, 33 Ma.

Maiacetus inuus a species of ancestral whales in the family Protocetidae. Notable for four flipper-like legs better for swimming than walking on land, *Maiacetus* evidently gave birth on land but spent most of its time in the water. Males grew to about 9 feet long, females 8 feet, and a fetal skeleton found with several other sets of remains is the only known fetal specimen of an ancestral whale. Pakistan, middle Eocene.

Maiasaura a genus of hadrosaurid ornithopod dinosaurs in the subfamily Saurolophinae. Up to 30 feet long, it was a medium-sized hadrosaur, but it is notable especially for indications that hatchlings were altricial, requiring some parental care. See also **Egg Mountain.** The United States, Late Cretaceous, 78–75 Ma.

Maiopatagium "mother of wings," a genus of gliding protomammals described in 2017, in the order Euharamiyida and family Eleutherodontidae. About 9 inches long, *M. furculiferum* had skeletal adaptations for gliding as well as a patagium. Not related to the earlier glider *Volaticotherium*, it had some mammalian traits but not others, such as the chain of ear bones that mammals developed for hearing. China, Late Jurassic, 160 Ma.

Majungasaurus a genus of large theropod dinosaurs in the family Abelisauridae; synonym *Majungatholus*. Known from several skulls and considerable skeletal material, it is estimated to have been 20–23 feet long, weighing about a ton. It seems especially closely related to abelisaurids from India. Madagascar, Late Cretaceous, 70–66 Ma.

Malacostraca a class of crustaceans that contains three subclasses: the Phyllocarida, Hoplocarida, and Eumalacostraca, the latter containing most of the familiar modern crustaceans. Cambrian to Recent.

Mamenchisaurus a genus of very large sauropod dinosaurs in the family Mamenchisauridae, discovered in 1952 by C.C. Young in the Sichuan province of China and known from several species found since then. The type species is *M. constructus*, notable for its very long neck, with large and elongated neck vertebrae; only *Sauroposeidon* is known to have a longer neck. Described in 1993, *M. sinocanadorum* grew up to 115 feet long, weighed between 50 and 75 tons, and had a neck up to 59 feet long. The length of the neck gave the family a long reach, but it is unclear whether they fed off high branches like a giraffe or kept their head close to the ground. Possible relatives are the slightly larger *Apatosaurus* (usually placed in the Diplodocidae) and *Argentinosaurus*. China, Late Jurassic.

Mammalodontidae a family of late Oligocene toothed mysticete whales. The two genera in the family are *Mammalodon* and *Janjucetus*, both about 10 feet long. Possessing synapomorphies of both odontocetes and mysticetes, the Mammalodontidae seem to represent one of the transitional steps from toothed to baleen whales; see also **Aetiocetidae** and ***Llanocetus***. Australia and New Zealand, known only from the late Oligocene.

Mammalia the class of mammals. The earliest stem-mammaliaforms appeared in the Late Triassic (see ***Eozostrodon*****, *Hadrocodium*****, *Kuehneotherium*****, and Morganucodonta**). They experienced a burst of evolutionary diversification early in the middle Jurassic and then spread worldwide with relatively little diversification for 100 million years until the end of the Mesozoic. Then in the Paleocene began the rapid diversification leading to their present dominance in the world. The principal characteristics that differentiate them from other vertebrates are mammary glands, generally fur or hair, three middle ear bones, a squamosal-dentary jaw joint, and a section of the brain called the neocortex.

Mammoth a general term used, sometimes interchangeably with mastodon, to refer to the extinct elephants of the Pleistocene, which are classified in the extant superfamily Elephantoidea and family Elephantidae. Some mammoths had upper and lower tusks as long as 7 feet and strikingly curved; they generally had more pointed skulls and more hair than modern elephants, and mammoth species ranged greatly in size. Found throughout North America, Africa, Europe, and Asia until recent times, the latest survived until about 7000 years ago.

Mammuthus trogonotherii the steppe mammoth, one of several genera of mammoths in the family Elephantidae that were larger than modern elephants; synonym *Mammuthus armeniacus*. Eurasia, Pleistocene.

Mammutoidea a suborder of proboscideans that includes the mastodons of the families Mammutidae and Stegodontidae. They are not directly related to modern elephants, but like the Elephantidae they had only upper tusks. Widespread in North America, Europe, Asia, and Africa in the Miocene; early Oligocene to Recent.

Maniraptora the clade of coelurosaurian dinosaurs that includes the birds and nonavian dinosaurs most closely related to them, principally the therizinosaurs, deinonychosaurs, and oviraptors. Their name refers to their grasping ability, facilitated by an easy-swiveling wrist. Global distribution, Late Jurassic to Recent.

Mansourasaurus shahinae a species of titanosaurian sauropod dinosaurs known from a partial skeleton found in Egypt and described in 2018. About 30 feet long, it was a medium-sized titanosaur that was not fully grown. The find is the most complete skeleton yet found of an African dinosaur from near the end of the Mesozoic. Late Cretaceous, 80 Ma.

Mantodea the mantises, an extant order of large insects in the superorder Dictyoptera. They have a sparse fossil record but are known from the Cretaceous. Global distribution, Early Cretaceous to Recent.

Mantophasmatidae an extant family of predatory insects in the order Notoptera, formerly considered a small order in its own right, called "Mantophasmatodea." The family is now known only in Southwestern Africa but was probably once widespread. It contains only half a dozen species, one a recently discovered living African insect and a similar one a few inches long, encased in amber, from the Eocene in Europe. These insects bear characteristics of the larger extant groups, the mantids and the phasmids. Europe and Africa, Eocene to Recent.

Manus plural manus; the distal part of the forelimb of vertebrates, corresponding to the human hand. The term manus includes the wrist and hand or carpus and forefoot.

Maotianshan Shales see **Chengjiang**.

Mapusaurus roseae a genus of very large theropod dinosaurs in the family Carcharodontosauridae. Discovered in western Patagonia in the late 1990s, it was perhaps the largest carnivorous dinosaur. As large as 40 feet and 3 tons, *Mapusaurus* probably preyed on *Argentinosaurus*, one of the largest of all dinosaurs, possibly hunting in packs. Known from several partial skeletons from the Cenomanian, between 97 and 94 Ma. Argentina, Late Cretaceous.

Marasuchus a monospecific genus of small dinosauriform archosaurs**;** synonym *Lagosuchus***.** Optionally bipedal and less than 2 feet long, *M. lilloensis* is one of

several early dinosauriforms close to the line of descent leading to the dinosaurs. Known from two specimens dated about 235 Ma, it had an asymmetrical trochanter at the point where the femur meets the hip, one of the defining characters of dinosaurs. Argentina, Late Triassic, 235–234 Ma.

Marattiaceae an extant family of eusporangiate ferns in the order Marattiales. Known from the Early Carboniferous to the present, several extant marattialean genera differ little from their Paleozoic ancestors. Global distribution, Early Mississippian to Recent.

Marble Canyon a second site of outcrops of the Burgess Shale Formation, in Kootenay National Park, about 24 miles south of the original site, which is known as the Walcott Quarry. Marble Canyon has yielded several specimens of new organisms, including several previously known only from the Chengjiang biota of China (see ***Misszhouia*** and ***Primicaris***). Roughly two-thirds of the taxa identified so far are known also from the Walcott Quarry, including the well-known *Marrella*, *Naraoia, Metaspriggina,* and *Liangshanella*, as well as the poorly known *Mollisonia* and *Oesia*. As at the Walcott Quarry, most of the specimens were deposited allochthonously and rapidly in fine-grained clay stones. The biota is dated at 508 Ma but may be slightly earlier than the original Burgess Shale biota. See also **Kootenayscolex.** Canada, middle Cambrian.

Marine transgression a long-term invasion of the sea over a large land area as a result of a warmer global climate and rising sea levels. Such transgressions were widespread in the Early Ordovician, and even more in the Cretaceous, when they created large epicontinental seas like the Western Interior Seaway of North America.

Marinoan Glaciation see **icehouse conditions.**

Mariopteris a genus of seed ferns in the family Medullosaceae. Its lianescent habit sets it off from the treelike growth of most seed ferns. Global distribution, Late Carboniferous to late Permian.

Marrella splendens a species of stem-group arthropods abundant in the Burgess Shale assemblage, an early arthropod in the family Marrellidae. The best-known of the marrellomorphs, it was only about an inch long and superficially resembles trilobites, but it had significant gill and appendage differences. Its appearance led Walcott to call it "lace crab" because of several long spines around its body. Canada, middle Cambrian, 508 Ma.

Marrellomorpha a subphylum of early arthropods considered to include three species of marrellids and several specimens called acercostracans. They are poorly known because of their lack of hard parts that could fossilize easily. North America, Europe, Asia, Africa, and Australia; early Cambrian to Devonian.

Marsupialia "pouch animals," mammals that bear young in a relatively undeveloped state, so that they must live for some time in an external pouch on the mother's chest, where they survive on milk secreted through the skin. Metatherian mammals, the ancestors of marsupials, probably diverged from the placental mammals in the Middle Jurassic, between 130 and 125 Ma. *Sinodelphys*, dated at 125 Ma, is known from China and is considered the earliest definitive metatherian fossil. The oldest definitive marsupial appeared in North America about 65 Ma, at the beginning of the Paleocene (see ***Peradectes***). Marsupials reached South America by the early Paleocene, where they diversified greatly while it was still part of Gondwana. They reached Australia via Antarctica shortly before those two continents separated in the early or middle Eocene, probably in a single dispersion event. Marsupials are extant in North and South America and Australasia.

Marsupites testudinarius an unusual species of large, purse-shaped articulate crinoids in the small order Uintacrinida. Stemless and with ten very long arms, *Marsupites* probably rested on the seabed, possibly embedded in sediment. Its calyx was about 2 inches wide and 3 inches high. The extinction of *M. testudinarius* is the boundary marker for the beginning of the Campanian Age of the Cretaceous. Cosmopolitan but best-known in England and the United States; Late Cretaceous, 84 Ma.

Masiakasaurus a monospecific genus of theropod dinosaurs in the family Noasauridae. Relatively small at 5–7 feet long, the bipedal *M. knopfleri* had short forelimbs and a long tail. It is notable for being the only known theropod with long, conical, hooked front teeth that protrude from the front of its mouth and may have been used to stab small prey. Madagascar, Late Cretaceous, 70–66 Ma.

Mass extinction see **extinction.**

Massospondylus a genus of plateosaurian sauropodomorph dinosaurs of the Early Jurassic. Optionally bipedal, 13–20 feet long, and weighing more than a ton, it had a sharp thumb claw on its small forelimbs. A large South African nesting site attributed to this dinosaur may be 100 million years older than the previous oldest dinosaur nest site. The eggs are 2–3 inches long and were found in clutches of up to three dozen eggs in ten nests. The discovery indicates earlier complex social behavior in dinosaurs than previously thought. Southern Africa, 190 Ma.

Mastodon a term sometimes confused with mammoth but referring more specifically to the slightly differentiated proboscideans of the extinct family Mammutidae and suborder Mammutoidea. North and Central America, late Miocene to late Pleistocene.

Mastodonsauroidea see **Capitosauroidea.**

Mastodonsaurus a genus of stereospondyl capitosaurian temnospondyls. Growing as long as 20 feet, *M. giganteus* is the largest-known temnospondyl, with a large head, eyes on top and midway in the skull, and a short tail. Europe, iddle Triassic.

Mastotermes electrodominicus a species of termites known from amber deposits of the Caribbean. Analysis of its DNA supports the view that termites and cockroaches have a common ancestor from which they evolved separately. Dominican Republic, Oligocene.

Materpiscis see **Gogo Formation**.

Mathildoidea an extant superfamily of heterobranch mollusks, superficially similar to the Terebridae and Turritellidae. Like the auger and tower shells, they are elongate and many-whorled but shorter and more slender. They differ also in other significant ways, including having an apertural notch and a sinistral protoconch, the first part of the shell to form. The families Tofanellidae and Gordenellidae are known worldwide from the Triassic to the Miocene, but the only extant family is the Mathildidae. Global distribution, Triassic to Recent.

Matoniaceae an extant family of ferns in the order Gleicheniales. After appearing in the Permian and spreading globally in the Jurassic and Cretaceous, the family disappeared from the Northern Hemisphere at the end of the Cretaceous. It was thought to be a Lazarus taxon because of three surviving genera in Southeast Asia, but it is now known from Cenozoic specimens from Antarctica, Argentina, Australia, and New Zealand. See also ***Weichselia.*** Permian to Recent.

Matrix the rock surrounding a specific fossil specimen.

Matthevia an enigmatic genus of small, chiton-like animals, tentatively considered polyplacophorans and placed in the order Paleoloricata. The United States and possibly Australia, late Cambrian to Early Ordovician.

Mawsonia a genus of large coelacanth fish in the family Mawsoniidae. The largest, *M. gigas*, was about 20 feet long and preyed on fish and large invertebrates. Africa and Brazil, Early Cretaceous, 110–100 Ma.

Maxakalisaurus topai a species of titanosaurian sauropodomorph dinosaurs. Probably related to *Saltasaurus*, it is estimated to be at least 40 feet long and weigh 9 tons. Notable for its osteoderms and vertical spine plates, it was herbivorous and had a small head and long neck and tail. Brazil, Late Cretaceous, about 80 Ma.

Mayomyzon pieckoensis a species of small, lamprey-like ostracoderms in the family Mayomyzontidae. It is known only from the Pennsylvanian assemblage of the Mazon Creek site. The United States, Late Carboniferous.

Mazon Creek a Konservat-Lagerstatten in northeastern Illinois where several coal mining sites, especially in the Francis Creek Shale, have produced very good fossils of about 500 species from the Late Carboniferous. The Mazon Creek deposits, laid down in a deltaic environment similar to the Grès à Voltzia of France, include terrestrial, freshwater, and marginally marine organisms from about 306 Ma, generally inside clay ironstone concretions. The most common fossils are insects, crustaceans, and other arthropods, as well as mollusks, jellyfish, and a variety of plants and trees. There are marine and freshwater bivalves but no corals or crinoids, and the only brachiopod is *Lingula*. Mazon Creek is known especially for the famous but enigmatic "Tully monster" (***Tullimonstrum**, q.v.*). The United States, Late Pennsylvanian.

Mecochirus a genus of decapod crustaceans in the family Mecochiridae. *Mecochirus longimanatus*, the type species, is notable for the extreme length of its first pair of walking legs. Several specimens in the Solnhofen deposits lie at the end of short trackways, evidently "death trails." Cosmopolitan, Jurassic to Cretaceous.

Mecoptera an extant order of neopteran insects, commonly called scorpionflies. Mecopterans may have been pollinators of gymnosperm plants before the appearance of the Hymenoptera in the early Mesozoic. Global distribution, Early Carboniferous to Recent.

Medullosaceae a family of seed ferns in the division Pteridospermatophyta and order Medullosales. It is the largest-known seed fern, growing more than 30 feet high, with large leaves and seeds. North America, Europe, Asia, and North Africa; Carboniferous to Permian.

Medusinites a disc-shaped Ediacaran fossil similar to the enigmatic *Aspidella*. Like *Aspidella*, it has been suggested as possibly ancestral to jellyfish. India, Norway, Algeria, Ukraine; Ediacaran.

Meemannia a genus of early actinopterygian fish. Considered a sister group of *Cheirolepis*, it is known only from a specimen found in China. Early Devonian (Lochkovian).

Megacerops a genus of perissodactyl mammals in the family Brontotheriidae. One of the larger brontotheres, the elephant-sized *Megacerops* stood about 8 feet high at the shoulder. It is also notable for a pair of blunt horns extending side by side from the nasal bone and the frontal bone. North America, late Eocene.

Megachirella wachtleri a species of lepidosaurian reptiles, stem-squamates tentatively placed in the clade Eolacertilia. Known from a single articulated specimen of a skull and spine about 3 inches long, *Megachirella* was identified in 2014 as the earliest-known squamate. It was first thought to be a more primitive lepidosaurian,

but careful examination showed a quadratojugal joint in the jaw as well as relatively modern, lizard-like wrist bones, arms, and shoulders. Italy, Middle Triassic, 240 Ma.

Megadactylus see ***Anchisaurus***.

Megafauna term used for large terrestrial mammals, especially of the Pleistocene. The defining weight threshold for the term varies between 100 and 1000 pounds.

Megalania see ***Varanus priscus***.

Megaloceros a genus of large deer in the subfamily Cervinae. *Megaloceros giganteus*, called "Irish elk," was almost 7 feet high at the shoulder and had a very heavy and wide (10 feet) set of antlers. The five species of *Megaloceros* inhabited Europe and Asia from the Pliocene to the end of the Pleistocene.

Megalochelys a genus of cryptodiran tortoises in the extant family Testudinidae. Weighing more than a ton, it is the largest-known land tortoise. South Asia, Miocene to Pleistocene.

Megalodon see ***Carcharodon*.**

Megalograptus a genus of large eurypterids in the suborder Eurypterina and family Megalograptidae. It was 4 feet long and had long, spiny claws and a long telson spine. North America, Early to Late Ordovician.

Megalolamna paradoxodon a proposed species of lamniform sharks in the family Otodontidae, known from 2-inch teeth found in scattered locations. Dated at 20 Ma, it seems to be a sister genus of the better-known *Otodus*. Peru, the United States, and Japan; known only from the Miocene.

Megalonychidae a family of large xenarthran ground sloths in the order Pilosa. The type genus *Megalonyx*, including the huge *M. jeffersonii*, was bearlike and could maneuver bipedally, standing 10 feet tall and weighing more than a ton. North and South America, Oligocene to the end of the Pleistocene.

Megaloptera an extant order of pterygote insects in the clade Neuropterida that includes the alderflies, dobsonflies, and fish flies. They are especially recognizable by their large wings, usually membranous and with a netlike venation; some extant species have a wingspan of almost 9 inches. Their fossil record is sparse, but they are known from the early Permian. Cosmopolitan, Permian to Recent.

Megalosauridae a family of tetanuran theropod dinosaurs. In addition to *Megalosaurus*, the family includes *Torvosaurus*, *Streptospondylus*, and probably *Sciurumimus*. North America, Europe, and Asia; Triassic to Cretaceous.

Megalosaurus bucklandii a species of large theropod dinosaurs, 23 feet long and bipedal, with short but robust forelimbs. It was one of the first formally identified dinosaurs, described in the 1820s and named by Georges Cuvier for William Buckland, the early English paleontologist. In creating the Dinosauria in 1842, Richard Owen referred to the theropod *Megalosaurus* and the nodosaurid *Hylaeosaurus* in addition to the better-known *Iguanodon*. England, Middle Jurassic.

Meganesia a biogeographic name for the large land mass that comprised Australia, Tasmania, and New Guinea during Pleistocene ice ages when the sea level was low enough for land bridges to join them together. They have been separated for the last 10,000 years, but the term is also sometimes used for the region of the present lands.

Meganeura monyi a species of giant predaceous griffinflies in the order Meganisoptera. It had a wingspan of 27 inches and a body length of 18 inches. Western Europe, Late Carboniferous to early Permian, 305–299 Ma.

Meganeuropsis permiana a species of giant griffinflies in the order Meganisoptera, with an estimated wingspan of 28–29 inches and a body length of 17 inches. North America, early Permian.

Meganisoptera an order of large-winged, predaceous insects, formerly called Protodonata. They were Carboniferous forerunners of the Odonata, the group that includes the modern dragonflies. Most were similar in size to modern dragonflies, but the order includes the largest-known flying insects, such as *Meganeura* and *Meganeuropsis*. Global distribution, Early Carboniferous to late Permian.

Megantereon a genus of early sabertooth cats in the subfamily Machairodontinae, probably ancestral to the later *Smilodon*. It weighed as much as 330 pounds, and its canine teeth were 3 inches long. North America, Africa, Europe, and Asia; early Pliocene (perhaps late Miocene) to middle Pleistocene.

Megatheriidae the largest ground sloths, a family of xenarthran mammals in the extant order Pilosa. Members of the family ranged in size from 6 to 20 feet long and weighed up to 4.5 tons. South America, late Oligocene to late Pleistocene.

Megatherium a genus of large mammals in the extant order Pilosa and extinct family Megatheriidae. It was the largest ground sloth, about 20 feet long and weighing more than 4 tons. *Megatherium* had three hooked claws on each foot and was primarily quadrupedal; it became extinct about 11,000 years ago, after the arrival of humans. South America, early Pliocene to late Pleistocene.

Megazostrodon a genus of small early stem-mammaliaforms in the family Megazostrodontidae. A scansorial insectivore between 4 and 5 inches long, it seems to represent one of the last transitional stages between the cynodonts and

true mammals. Although it was oviparous and had some other reptilian features, *Megazostrodon* had mammalian ear bones, mammalian fur and vibrissae, and a heterodont dentition of four types of teeth. Its name, "large girdle tooth," derives from the prominent ridges on its molars. Elliot Formation, South Africa, Late Triassic to Early Jurassic.

Megistaspis a diverse genus of burrowing trilobites in the family Asaphidae. It was generally distinguished by a pointed cephalon, and some species were pointed at both ends, with a pointed cephalon and also a spiked telson. North and South America, Australia, Europe, and Asia; Early to Middle Ordovician.

Megistaspis acuticauda a species of large burrowing trilobites in the family Asaphidae. It was more than a foot long and had a distinctive pointed cephalon and a shorter pointed telson. North America, Europe, Asia, and Australia; Early Ordovician.

Mei long "sleeping dragon," a species of small troodontid dinosaurs in the Jehol biota. A basal troodontid; it is almost 3 feet long, with winglike arms and long, clawed fingers. It is known from two well-preserved specimens, both found in a birdlike sleeping posture; neither has obvious feathers but may have had a feather-like coating. China, Early Cretaceous, 125 Ma.

Melanopsis a genus of Miocene gastropod mollusks notable for its evolutionary stasis for 7 million years, followed by a period of rapid change for 2 million years as the environment changed from marine to freshwater. In this period the shell size increased and a distinctive shouldering pattern evolved. Europe and Asia, Miocene.

Melanorosaurus a genus of early sauropodomorph dinosaurs in the family Melanorosauridae. Quadrupedal, with massive, sauropod-like limbs; it was about 26 feet long and weighed a little more than a ton. *Melanorosaurus* is dated about 210 Ma, close to its relative *Antetonitrus.* South Africa, Late Triassic.

Melittosphex burmensis a species of bees in the family Melittosphecidae. Preserved in amber, it is the earliest-known specimen of a bee, dated at 99–100 Ma. Burma, Early Cretaceous.

Meniscotherium a genus of herbivorous protoungulate mammals in the family Phenacodontidae. Ranging from 15 to 30 pounds, they had hooves and the selenodont teeth of ruminant herbivores. North America, Eocene.

Menoceras a genus of perissodactyl mammals in the family Rhinocerotidae. Known from two dozen specimens, it was about 5 feet long, smaller than its relative *Diceratherium*. Males had the same unusual pair of side-by-side nasal horns as *Diceratherium*. North America as far south as Panama, late Oligocene to early Miocene.

Meraspis the intermediate growth phase of trilobites, during which the thorax and pygidium became distinct; see also **protaspis** and **holaspis**.

Merostomata an obsolete term for a class of chelicerate arthropods that was considered to include the extinct order Eurypterida and the extant Xiphosura. The latter are now sometimes regarded as a class in their own right. Middle Ordovician to Recent.

Merychippus a genus of three-toed Miocene horses in the family Equidae, the first known grazing horse. At 3 feet high, it was the tallest horse of the time. It had three toes and was much more horselike in appearance than its ancestors, although still small. *Merychippus* probably gave rise to several other genera of grazers, such as the three-toed *Protohippus* and the more successful *Hipparion*. North America, early to late Miocene.

Merycoidodontidae a large family of artiodactyl ruminants in the extant suborder Tylopoda and extinct superfamily Merycoidodontoidea, previously called Oreodontidae. They were browsers with a selenodont dentition and claws instead of hooves. Abundant in the Oligocene, they were piglike in appearance but are generally considered camelids. North America from Oregon to Central America, late Eocene to Miocene.

Mesacanthus a genus of primitive acanthodian fish in the family Acanthodidae. Ranging from a few inches to a foot in length, *Mesacanthus* is characterized by pectoral, anal, pelvic, and dorsal fin spines. Its name derives from an unusual pair of pre-pelvic fins in the middle of the body. Scotland, Early to Middle Devonian.

Mesocyon a species of doglike mammals in the family Canidae and subfamily Hesperocyoninae, related to *Cynodesmus*. Weighing about 16 pounds, it is known only from sites in Oregon, California, Colorado, and Nebraska. Western North America, early Oligocene to early Miocene.

Mesogastropoda a discarded term formerly used for many prosobranch gastropods that seemed to be more advanced than the Archaeogastropoda (now also discarded).

Mesohippus a genus of early Equidae in the extinct subfamily Anchitheriinae. It was slightly larger than *Hyracotherium* but still only about 2 feet high at the shoulder. A cousin, *Anchitherium*, migrated to Eurasia in the early Miocene, becoming extinct in the Pliocene. North America, late Eocene to early Oligocene.

Mesolimulus a genus of xiphosurans in the family Limulidae. Almost identical to the modern horseshoe crab, several specimens of *Mesolimulus* are known from the Solnhofen quarries, including a famous one that died at the end of a well-preserved 30-foot trackway. Europe, Late Jurassic 151–146 Ma.

Mesolobus a genus of small articulate strophomenate brachiopods in the order Productida. Almost rectangular, *Mesolobus* is 0.3 inches long and 0.6 inches wide, with a wide, straight hinge line. It has a shallow fold on the brachial valve and very fine ribbing and growth lines. North America, Russia, and China; Carboniferous to middle or late Permian.

Mesonychidae a family of protoungulate mammals in the order Mesonychia, related to a variety of modern mammals, including whales, hippopotamuses, and dolphins. Although they were long thought to be direct ancestors of whales, their relationship is now thought to be more distant. Ranging from 3 to 13 feet in length and having four-clawed feet, the mesonychids encompassed a wide variety of herbivores and carnivores. They declined in the Eocene, with only one genus, *Mongolestes*, surviving into the Oligocene. Europe, Asia, and North America; early Paleocene to early Oligocene.

Mesonyx a genus of carnivorous mammals in the family Mesonychidae. Wolflike in appearance and behavior although not directly related to canids, *Mesonyx* grew to about 5 feet long, excluding its tail. North America and Asia, late Eocene.

Mesophyticum term sometimes used for a paleobotanic division of time roughly corresponding to the Mesozoic Era and characterized by the plant life of the Mesozoic.

Mesopsychopsis a genus of lacewings, neuropteran insects in the family Brongniartiellidae. It was about 1 inch long, with fine wing venation. Germany, Early to Late Jurassic.

Mesosauria a single-family order of small aquatic reptiles, also called Proganosauria. Their taxonomic position is controversial, some considering them basal "parareptiles," others preferring to place them in the stem-reptile family Captorhinidae and some even claiming similarities to synapsids. They are the earliest-known aquatic reptiles, possibly descended from terrestrial ancestors, and may be the earliest-known viviparous reptiles. From 2- to 3-feet-long and broadly resembling modern crocodiles, they probably inhabited a saltwater basin where southern Africa and South America were still joined in the early Permian.

Mesosaurus a genus of aquatic reptiles in the family Mesosauridae. About 3 feet long, its small skull had a narrow jaw with many needle-sharp teeth, and it had a long tail and webbed feet. South America and southern Africa, early Permian.

Mesosuchians a large paraphyletic grouping of archaic terrestrial or semiaquatic reptiles, generally placed in the superorder Crocodylomorpha. Widespread in the Jurassic and Cretaceous, they had elongated and flattened skulls, and some genera had very long tails. Global distribution, Early Jurassic to Eocene.

Mesothelae a primitive suborder of arachnids, spiders in the order Araneae, with only one extant representative, the Liphistiidae of East Asia. For the earliest mesothele, see ***Palaeothele***. The principal difference from the more advanced Opisthothelae is the segmented body of the Mesothelae; another primitive trait is their four book lungs, which are absent or reduced in opisthotheles. The Mesothelae include most of the earliest spiders, known from North America and Europe from the Late Carboniferous and Permian to Recent.

Mesozoic Era See **Geologic Time Scale.**

Mesozoic Marine Revolution Early in the Mesozoic Era, several marine predators developed new, durophagous shell-crushing abilities: first the placodont marine reptiles in the Triassic, then the ichthyosaurs, and in the Cretaceous the mosasaurs and ptychodontid sharks. Because of the resulting increase in durophagy, the populations of crinoids, brachiopods, and ammonoids and other gastropods decreased rapidly. The character of the benthos was changed greatly, with many sessile and slow-moving taxa becoming extinct. Some species developed new protections, such as lighter, streamlined bodies that could escape by swimming or jet propulsion. Bivalves survived better than brachiopods, mainly by burrowing and becoming infaunal; some, such as the Pectinidae, developed the ability to jump away from predators.

Messel Shale Pit an Eocene Konservat-Lagerstatten near Frankfurt am Main. Representing a complete lakeside ecosystem in a subtropical forest, it has yielded a great variety of fossils, including especially mammals but also plants, insects, and other arthropods and invertebrates. The 35 mammal species include *Darwinius masillae*, possibly a primitive primate, and the very unusual *Leptictidium*. See also ***Palaeopython***. Germany, early Eocene, 49 Ma.

Messinian Event (also known as the Messinian Salinity Crisis). The drying up of the Mediterranean Sea at the end of the final age of the Miocene (the Messinian), from 5.96 to 5.33 Ma; the causes are unclear.

Metacopina a suborder of ostracods generally placed in the order Podocopida. Their carapaces have features that seem to be transitional between the other two podocopid suborders, the Platycopina and the Podocopina. Widespread in the late Paleozoic, surviving the end-Permian extinction, and thriving through most of the Early Jurassic, the Metacopina became extinct relatively abruptly toward the end of the Early Jurassic. The reasons for their disappearance are unclear, the strongest hypothesis pointing to their replacement by more advanced ostracods. Global distribution, Middle Ordovician to Early Jurassic, 460–180 Ma.

Metaplacenticeras a genus of ammonoids in the order Ammonitida and family Placenticeratidae. *Metaplacenticeras* is important as an index fossil for the late Campanian. Japan, California, and Antarctica; Late Cretaceous.

Metasequoia a genus of deciduous redwoods in the family Cupressaceae, with one species (*M. glyptostroboides*) still living in China, unchanged since the Cretaceous. Originating in the Middle Cretaceous, *Metasequoia* forests in three genera were found at high latitudes across the Northern Hemisphere from the Paleocene to the Miocene.

Metaspriggina walcotti a species of very primitive chordates known from both sites of the Burgess Shale. It was so named because of a superficial similarity to the Ediacaran genus *Spriggina*, but the two are now thought to be unrelated. *Metaspriggina* is now considered a craniate and possibly a primitive fish. Canada, middle Cambrian, 508 Ma.

Metastigmata see **Ixodida**.

Metatarsals the bones between the toes and the rear of the foot of birds, reptiles, and mammals, usually forming the central part of the foot.

Metatheria an infraclass of therian mammals that includes all marsupials, extinct and living. Although they probably diverged from placental mammals in the Jurassic, the earliest-known metatherian fossils, such as *Sinodelphys szalayi*, have been found in Cretaceous sites in China. The first true marsupials are found in lower Paleocene strata in North America (see ***Peradectes***). Migrating into South America, probably near the end of the Cretaceous, marsupials then spread through Gondwana, appearing in Europe and North Africa in the Eocene. They reached Australia in the early or middle Eocene, shortly before it separated from Antarctica.

Metazoan an animal that has evolved beyond the one-celled stage, having a complex cell structure and nervous system. Metazoans are widespread and diverse in early Cambrian deposits, and putative but uncertain metazoans abound in the Ediacaran biota.

Metoldobotes see **Macroscelidea**.

Metoposaurus a genus of large temnospondyl amphibians in the suborder Stereospondyli and family Metoposauridae, possibly close to the ancestral stock of modern amphibians. Up to 10 feet long, the salamander-like *Metoposaurus* occupied a crocodile-like niche, feeding mainly on fish. The genus includes *M. diagnosticus algarvensis* (discovered in Portugal in 2015) and three other members. Europe, Late Triassic, 230–200 Ma.

Metrarabdotos an extant, species-rich genus of bryozoans in the order Cheilostomata. It is often noted as an example of punctuated equilibrium: some species are known to have evolved rapidly into new species without intermediate forms after as long as 16 million years of static, unchanging existence. North America and Europe, Oligocene to Recent.

Metriacanthosauridae a family of theropod dinosaurs in the superfamily Allosauroidea; synonym Sinraptoridae. The family is named for its moderately high neural spines, which probably supported strong hip, back, and neck muscles and may have had other functions as well. Here they are lower than in the highest-spined carnosaurs such as *Acrocanthosaurus*, but higher than in *Allosaurus*. Estimated dates vary widely between 175 and 94 Ma; the family is thought to have originated in Asia and migrated to Europe. Asia, Europe, and Africa; Late Jurassic to Late Cretaceous.

Metriacanthosaurus a genus of theropod dinosaurs in the family Metriacanthosauridae. A medium-sized theropod, estimated at 17–20 feet long; it had three digits on each manus and was bipedal. England, Middle Jurassic, 160 Ma.

Metriorhynchidae a family of marine crocodylomorphs in the clade Thalattosuchia. The type species *Metriorhynchus* ("moderate snout") is about 10 feet long with a streamlined body, paddle-like forelimbs, and a tail fin. North and South America and Europe; Middle Jurassic to Early Cretaceous.

Miacis a genus of arboreal carnivores in the extinct superfamily Miacoidea and family Miacidae. Close to the ancestry of modern carnivores, the weasel-sized *Miacis* descended from insectivores and had a larger brain than its cousins the creodonts. North America, Europe, and Asia; late Paleocene to late Eocene.

Michelinia a genus of colonial favositid corals in the order Tabulata; global distribution, Early Devonian to late Permian.

Micraster an evolutionarily important genus of irregular atelostomate echinoids in the extant subclass Euechinoidea and order Spatangoida. Characterized by its heart shape, a dense covering of small tubercles which supported a forest of short spines, and five deeply sunken ambulacra, the 2-inch-wide *Micraster* lived in a burrow in marine sediment. Study of the gradually evolving changes in species of *Micraster* in 10 million years (almost 500 feet) of the chalk beds of the Late Cretaceous made it well-known in the nineteenth century as an example of evolution. North America, Europe, Africa, and Antarctica; Late Cretaceous to Paleocene.

Microcystis a genus of freshwater cyanobacteria that can produce algal blooms with toxins that cause anoxia; global distribution, Permian to Recent.

Microdictyon a genus of enigmatic wormlike animals. See ***M. sinicum***. Tommotian biota, global distribution, early Cambrian.

Microdictyon sinicum a species of wormlike animals so far unrelated to later taxa but considered a possibly basal onychophoran. Its discovery in 1989 is remarkable for solving the mystery of small, round phosphatic caps called *Microdictyon* that were one of the enigmatic elements of the small, shelly fauna. These caps covered

the joints where the ten pairs of leglike appendages joined the body of the animal. It is now known from several complete body fossil specimens. China, Chengjiang biota, early Cambrian, ca. 518 Ma.

Microdomatidae a family of marine gastropods in the superfamily Trochoidea. This family of high-spired sea snails includes the subfamilies Microdomatinae and Decorospirinae. North America, Asia, and Europe; Early Devonian to Early Triassic.

Microfossil a fossil whose typical form is microscopic in size. Because they are so abundant and rapidly evolving, many microfossils are extremely useful in biostratigraphy. Some of the more important groups are the diatoms, Foraminifera, Radiolaria, and other protists.

Micromelerpetidae a family of temnospondyl amphibians in the superfamily Dissorophoidea. Europe, Late Carboniferous to Early Triassic.

Micropaleontology the branch of paleontology dealing with fossils that require a microscope to see their form and important characteristics.

Microraptor a genus of small (less than 3 feet long but only 2 pounds), carnivorous feathered dinosaurs in the family Dromaeosauridae, known from many specimens recovered in the Jiufotang Formation of Liaoning. Synonym *Cryptovolans pauli*. It had feathers on forelimbs and hind limbs, which may have been used for short glides or flights. A 2012 study argues from comparisons of melanosomes with modern birds that the feathers were probably iridescent. China, Early Cretaceous, 125–113 Ma.

Microsauria a large order of amphibians in the subclass Lepospondyli. The microsaurs all had short tails and small legs but otherwise differed widely in form and habit, some being primarily aquatic and others primarily terrestrial. North America and Europe; Late Carboniferous to late Permian.

Microsyopidae a family of early primates in the extinct suborder Plesiadapiformes; the type genus is *Microsyops*. North America and China, late Paleocene to middle Eocene.

Microtheriomys brevirhinus a small species of beaver, living about 28 Ma, that seems to be closely related to the modern beaver. It was discovered in the John Day Fossil Beds in Oregon in 2014, where several other beaver species have been found. The United States, Oligocene.

Microtragulus a genus of marsupials in the extinct family Argyrolagidae. The omnivorous *Microtragulus* resembled a small kangaroo. South America, late Miocene to Pleistocene.

Middle Awash an important site in Ethiopia for hominid and hominin fossils during the period between 5 and 2.5 Ma. A series of important fossils have been found here within a few surface miles of each other. The fossils, which have been found by different collectors over the last few decades and may or may not be directly related to each other, include several specimens each of the early *Ardipithecus ramidus* (about 4.4 Ma) and the later *Australopithecus anamensis* (about 4.2 Ma) and *A. garhi* (2.5 Ma).

Milleporidae an extant family of cnidarians in the class Hydrozoa and order Capitata, commonly called fire corals for their powerful sting, but not true corals. They form colonies of soft-bodied polyps but, like the stylasterines, differ from other Hydrozoa in having calcareous parts that fossilize. Global distribution, Cretaceous to Recent.

Millerettidae a family of small, lizard-like parareptiles. The insectivorous millerettids are probably related to *Eunotosaurus* and possibly to the pareiasaurs. Southern Africa, late Permian, 259–252 Ma.

Mimicry see **Batesian mimicry.**

Miniaturization see **Kinorhyncha** and **Loricifera.**

Miocene the fourth epoch of the Cenozoic Era, from 23 to 5.3 Ma. After the numerous extinctions of archaic mammals at the end of the Oligocene, the Miocene saw the almost global radiation of all modern mammals. If *Ardipithecus kadabba* is confirmed, it will mark the end of the Miocene, between 5.8 and 5.3 Ma, as the first appearance of hominins.

Although grasses appeared much earlier, in the late Paleocene, they did not spread rapidly until the end of the Oligocene. The early Miocene is characterized by an accelerated change from lush forests toward open grassland, so that by the end of the period, open and wooded grassland communities were common worldwide. Ungulates in the Miocene evolved in response, developing specialized teeth for grazing the tough grasses, as well as longer limbs to enable escape from predators in the open country.

The northern continents saw considerable interchange of animals, but South America and Australia continued to be isolated, developing many eccentric groups.

Miocidaris a genus of pencil echinoids in the extant order Cidaroida and the type genus of the family Miocidaridae. *Miocidaris* was one of the few cidaroids that survived the end-Permian extinction. North America, Europe, and Asia; late Permian to Early Jurassic.

Miopetaurista a genus of gliding mammals in the family Sciuridae and subfamily Pteromyinae. Several species are known between the Miocene and Pliocene, mainly from Europe but also from China and the United States. Their head and body length

was up to 18 inches, with a tail as long. The Miocene species, such as *M. neogrivensis*, are extremely similar in size and morphology to the extant genus *Petaurista*, with wrist bones that are highly adapted to be able to stretch the patagium. Europe, China, and the United States; middle Miocene to Pliocene.

Mioplosus a genus of actinopterygian fish in the extant family Percidae. Up to 20 inches long, they were significant predators. Global distribution, early to late Eocene.

Miosireninae one of several extinct subfamilies in the sirenian family Dugongidae; Europe, Africa, and North America; Oligocene to Miocene.

Misliya the location of a cave in Israel where a partial upper jawbone was found that is considered the earliest evidence of modern humans outside Africa. Its date is estimated at between 194,000 and 177,000 years ago.

Mississippian see **Carboniferous.**

Misszhouia a monospecific genus of nektaspid arthropods in the family Naraoiidae. *M. longicaudata* was first found in the Chengjiang biota and then in 2014 at the Marble Canyon site of the Burgess Shale. The latter discovery, along with that of *Primicaris*, also at Marble Canyon, extends its paleogeographic and temporal range considerably. Along with the similar assemblages found at Fezouata, Morocco (more than 25 million years later than the Burgess Shale biota), and in the Chengjiang biota (7–10 million years earlier than the Burgess Shale), these discoveries indicate a greater longevity than previously thought for many early Paleozoic organisms. China and Canada, early to middle Cambrian, 518–508 Ma.

Mistaken Point an important Konservat-Lagerstatten in exposed surfaces of argillites on the Avalon Peninsula in Newfoundland. A rich Ediacaran assemblage of several types of fossils was preserved here by a blanket of volcanic ash, dated at about 565 Ma. Among the prominent specimens are *Bradgatia*, *Charniodiscus*, and the rangeomorph *Fractofusus misrai*. Some are similar to specimens found in Russia and Australia, while others are unknown except at Mistaken Point. Canada, Ediacaran, 575–560 Ma.

Mitosis the process of cell division by which cells in living organisms multiply. The process is almost identical in plants and animals, evidence that both are descended from a common ancestor. Current evidence predicts that this common ancestor was a one-celled organism that lived about 1.5 billion years ago.

Mixodectidae a family of insectivorous placental mammals in the order Dermoptera, called "mixed biters" for their combination of traits that may be transitional between early and later placentals. Their postcranial arboreal adapta-

tions are similar to the modern colugo. North America, Late Cretaceous to early Eocene.

Mixosaurus "mixed lizard," a genus of ichthyosaurs in the family Mixosauridae. A medium-sized ichthyosaur 3–6 feet long and the most common of the Triassic, *Mixosaurus* represents a transitional form between earlier, eellike forms and the porpoise-like ichthyosaurs of the Late Triassic. Global distribution, Middle Triassic.

Mixotoxodon a genus of notoungulates in the family Toxodontidae. The size of a rhinoceros and weighing about 4 tons, it was the largest notoungulate and had a combination of traits characteristic of different toxodontids. South, Central, and North America; middle to late Pleistocene, the latest specimen dated at around 25,000 years ago.

Moa see **Dinornithidae.**

Mobergellidae a family of small shelled organisms in the "small, shelly fossil" group. *Mobergella* has a circular cap or shell bearing muscle scars, possibly a monoplacophoran but similar to the Kirengellidae. Known especially from Scandinavia, early Cambrian.

Modern synthesis the consensus view of evolutionary theory that developed in the early to middle twentieth century and was almost universally accepted between 1950 and 1970. The term itself was made popular in the 1940s by Julian Huxley's *Evolution: The Modern Synthesis*, which presented the combination of Darwinian evolution with modern genetics that was being developed by scientists such as Ernst Mayr, Theodosius Dobzhansky, and G. G. Simpson. This view stresses **phyletic gradualism** (*q.v.*) and steady evolutionary change by natural selection. It gave little attention to the effects of catastrophic events and mass extinctions. See also **uniformitarianism**.

Modiolopsis a genus of Paleozoic marine bivalves in the order Modiomorphida and family Modiomorphidae. About 1.5 inches long, its outline is suboval, with slightly asymmetrical valves; the thin shell has fine, concentric growth lines. Stratigraphically important in the Ordovician. Global distribution, Early Ordovician to late Permian.

Modiolus an extant genus of medium-sized bivalve mollusks in the family Mytilidae and subclass Pteriomorphia. A burrowing mussel; it attached itself byssally to debris in sediment. Global distribution, Early Devonian to Recent.

Modular or mosaic evolution a model of evolutionary change that claims that different rates of change may occur in various body structures or functions, that is, that a change in one body part may occur without simultaneous changes in other body parts. It focuses on organisms in which advanced anatomical components are

combined with primitive components. The wukongopterid pterosaurs seem to be a good example. See also **correlated progression model**.

Moeritheriidae a family of piglike mammals in the order Proboscidea. Although the moeritheres resemble tapirs and pygmy hippopotamuses, they are not related. They are probably not ancestors of elephants either, but a separate extinct branch of proboscideans. They were trunkless but bore long canines that can be considered small tusks. North Africa, late Eocene.

Mold an impression left by a dead organism in soft material that has solidified. An external mold is an impression of an organism's body in surrounding sediment or volcanic material, the surrounding walls of which are left after the organism decomposes; the resulting mold is necessarily found in pieces. An internal mold is formed by material filling a void created by decay of the soft parts of an organism, resulting in a cast that resembles the shape of the body part and may preserve some of the external details.

Molecular paleontology study of fossilized remains at the molecular level, focusing on genetic material such as DNA. Investigators have identified possibly viable genetic material in insects preserved in amber as old as the middle Paleocene. Molecular techniques have been important in research on such species as the *Quagga*, on hominins such as *Homo heidelbergensis* and the *Denisovans*, on dinosaurs such as *Diplodocus hallorum*, and even older organisms. Some investigators advocate trying to recreate extinct organisms from this genetic material.

Mollisonia a genus of small arthropod-like organisms known only from the Burgess Shale and Chengjiang Lagerstätten. From 1 to 3 inches long, it had several segments, but little else can be discerned so far from the few specimens found. Canada and China, early to middle Cambrian.

Mollusca a large and very diverse phylum of marine and freshwater organisms. The most prominent extant classes are the Bivalvia, Gastropoda, Cephalopoda, Polyplacophora (Amphineura), Monoplacophora, Aplacophora, and Scaphopoda. Two other classes are extinct and important in the fossil record: Rostroconchia and Helcionelloida. The principal defining traits of mollusks are a muscular mantle, a rasping radula, and a definitive nervous system. Global distribution, Cambrian to Recent.

Molteno Formation an Upper Triassic formation in the Karoo Basin. Its fossils include several genera of the seed-fern *Dicroidium*, rare spiders, and many insects and conchostracans. South Africa, Late Triassic, 229–223 Ma.

Mongolarachne jurassica a species of araneomorph spiders in the family Mongolarachnidae**;** originally called *Nephila jurassica*. Known from male and female specimens, *Mongolarachne* is considered a stem-orbicularian; it is the larg-

est fossil spider yet found, with a body length of an inch and a leg span of 2.5 inches. It produced cribellate silk and is probably related to the deinopoids. China, Late Jurassic, 165–156 Ma.

Mongolestes a genus of protoungulate mammals in the family Mesonychidae. The last surviving mesonychid, *Mongolestes*, was about 7 feet long and had larger teeth than others in the family. Mongolia, Eocene to early Oligocene.

Monobathrida a large order of generally pelmatozoan monocyclic crinoids in the order Camerata; global distribution, Early Ordovician to late Permian.

Monoclonius a dubious genus of ceratopsian dinosaurs usually classified in the subfamily Centrosaurinae. About 17 feet long and 6 feet high, it may have had one long horn on its beaked snout. Known only from incomplete remains, some of which have been lost and some reclassified, *Monoclonius* is probably a *nomen dubium*. North America, Late Cretaceous, 77–75 Ma.

Monocyathida a class of archaeocyathans with only a single porous wall, usually solitary; Australia, Antarctica, North America, Asia, and Europe; middle Cambrian.

Monograptid fauna an important graptolite fauna, generally with a single stipe, representing the graptoloids' tendency toward scandent growth and fewer stipes. See **Graptolithina**. Early Silurian to Early Devonian.

Monograptus a genus of graptoloids in the family Monograptidae. Scandent, generally with a single straight stipe with hooked thecae. The first appearance of *M. uniformis* marks the GSSP at the base of the Lochkovian Epoch (419.2 Ma), the beginning of the Early Devonian. Global distribution, early Silurian to Early Devonian.

Mononykus olecranus "single claw," a unique species of theropod dinosaurs in the family Alvarezsauridae. Known from only one partial specimen, *Mononykus* was about 3 feet long and lightly built, with slender legs. It had very short but robust forelimbs, equipped with only one 3 inch claw, which may have been adaptations for hunting mound-living insects. Nemegt Formation, Mongolia, Late Cretaceous, 70 Ma.

Monophyletic group a clade, a group of organisms consisting of an ancestor and all of its descendants; see also **polyphyletic group**.

Monophyllites a genus of ammonoids in the order Phylloceratida and family Ussuritidae. Thin and evolute, *Monophyllites* was 3–5 inches across. Asia, Europe, North America, and New Zealand; Middle to Late Triassic.

Monophyodonty see **dentition**.

Monoplacophora a primitive but extant group of mollusks with single, limpet-like shells. It is generally considered polyphyletic, but the fossil record is sparse and leaves many questions open; in some classifications, the monoplacophorans are included in the Gastropoda despite considerable anatomical differences. They also have some features similar to segmented worms. The living monoplacophorans, such as *Neopilina*, are bottom-feeders in deep-ocean water. Cosmopolitan, early Cambrian to Recent.

Monotremata "single-hole," an extant order of egg-laying mammals. Once widespread, the monotremes are now restricted to the platypus and echidna of Australia and New Guinea. They display reptilian, avian, and mammalian traits, including a cloaca through which the urinary, intestinal, and reproductive tracts all open to the outside, rather than having separate urogenital and intestinal openings. Their fossil record is sparse, with the earliest dated in the Early Cretaceous (see ***Steropodon***), but they were probably widespread in Gondwana earlier in the Mesozoic. Australia, New Guinea, and possibly Madagascar and Argentina; Early Cretaceous to Recent.

Montanalestes a poorly known genus of small mammals tentatively placed in the clade Eutheria. Known only from jaw fragments and six embedded teeth, it seems closely related to later eutherians. The United States, Early Cretaceous, 110–100 Ma.

Montceau-les-Mines a Konservat-Lagerstatten in central France. It is noted for flattened and three-dimensional fossils of a tropical biota, including pteridosperms, insects, arachnids and other chelicerates, and tetrapods. France, Late Carboniferous.

Monticulipora a genus of stenolaemate bryozoans in the order Trepostomata. It formed massive colonies, sometimes encrusting brachiopods. North and South America and Europe, Late Ordovician.

Montlivaltia a genus of large, solitary scleractinian corals in the family Montlivaltiidae, up to 4 inches across, cylindrical or flattened, with a ridged exterior. Global distribution, Triassic to Pliocene.

Morganucodon a genus of advanced mouse-like cynodonts in the family Morganucodontidae. One of the earliest true mammals; it was about 4 inches long and probably omnivorous, and it had a long snout, a double jaw joint, and a heterodont dentition. See also ***Eozostrodon***. Best known from Glamorgan County, Wales, but found also in North America, Europe, and Asia; Late Triassic to Middle Jurassic.

Morganucodonta a clade of early mammaliaform cynodonts, perhaps the first true mammals. The morganucodonts were shrew-sized and slender, with a relatively large head, and they probably had a good sense of smell. Their dentition resembled that of modern mammals: the teeth were diphyodont and also specialized, with different types of teeth. They had strong jaws that were able to crush insects with stiff

exoskeletons, but they also had specialized teeth able to tear flesh. Wales, Europe, Africa, North America, and Asia; Late Triassic to Early Cretaceous.

Moropus "slow foot," a genus of clawed perissodactyl mammals in the superfamily Chalicotherioidea. Found from Oregon to Florida in the United States throughout the Miocene, *Moropus* was more similar to horses than other chalicotheres. As its name indicates, it walked awkwardly because of its large forelimb claws. It stood about 8 feet high at the shoulder and weighed up to 600 pounds. The United States, Miocene.

Moros intrepidus a species of theropod dinosaurs, the earliest-known tyrannosauroid of North America. Estimated at 13–15 feet long (half of it the tail) but less than 200 pounds, it is known from an almost-complete hind limb found in central Utah and described in 2019. The United States, Late Cretaceous, 96–95 Ma.

Morotopithecus a genus of Miocene hominoids described in 2004 and dated at 20.6 Ma or earlier. Known from dental, hip, and shoulder fragments, *Morotopithecus* may be transitional between the apes of the Miocene and more advanced hominoids. Uganda, early Miocene.

Morrison Formation a geologic formation in the Rocky Mountains of North America, stretching west from Kansas to central Utah and from New Mexico up to southern Alberta and Saskatchewan. The Morrison Basin fossils, most famous for many species of dinosaurs, comprise a complete community of terrestrial life in the Kimmeridgian and Tithonian Ages at the end of the Late Jurassic. Almost all locations are fluviatile or lacustrine, with almost no marine strata. Important dinosaur specimens have been found at many outcrops of the formation, but the largest Konzentrat-Lagerstätten are Utah's Dinosaur National Monument and Cleveland-Lloyd Dinosaur Quarry, Wyoming's Como Bluff**,** and Colorado's Dry Mesa Dinosaur Quarry.

Mosasauridae a family of large marine reptiles in the order Squamata and extinct superfamily Mosasauroidea. They probably evolved from the smaller, less specialized aigialosaurs in the Early Cretaceous and diversified worldwide to become the dominant marine predators, becoming extinct at the end of the period. First found in 1764 at Maastricht on the Meuse River, mosasaurs were air-breathing and ranged from 3 to 60 feet long.

Powerful swimmers, they have the body shape of a streamlined varanid, such as the modern monitor lizards, to which they are closely related. They preyed on fish of all sizes, sharks, ammonoids, turtles, and sea birds. They had double-hinged jaws, gulping down small prey whole; some species had two large teeth pointing backward down the throat to prevent prey from escaping. Others, such as *Globidens* and *Prognathodon*, had blunt, rounded teeth adapted to crushing ammonoids and bivalves. Some species had heterocercal tail fins, but a paucity of complete speci-

mens leaves their mode of swimming uncertain. They were covered with scales, and the presence of melanin in their skin indicates possible countershading like that of many modern fish (dark above and light below). Global distribution, Early to Late Cretaceous.

Mosasaurus hoffmanni the type species and the largest of the genus, *M. hoffmanni* was as much as 56 feet long and had jaws about 40 inches long. Late Cretaceous, 70–66 Ma.

Moschops a poorly known genus of dinocephalian therapsids in the family Tapinocephalidae. Massively built, especially in the skull, with long, stout teeth adapted for a herbivorous diet. Known only from the Karoo Basin of South Africa, middle to late Permian.

Moschorhinus a genus of therocephalian therapsids in the family Akidnognathidae. It was carnivorous and about 4.5 feet long, with a large head and a short tail. One of the few therocephalians that survived the Permian extinction, *Moschorhinus* specimens of the Triassic exemplify the Lilliput effect of smaller size in a species after a mass extinction. Karoo Basin, South Africa; late Permian to Early Triassic.

Mosineia a genus of arthropods in the family Euthycarcinidae. Three post-abdominal exoskeletons are the only specimens of the well-known *M. macnaughtoni*, one of the body fossils of early arthropods found along with their trackways in Cambrian strata in Wisconsin and Quebec. Probably amphibious, they may be the earliest animals to walk on land. See also ***Pneumodesmus*** and **Blackberry Hill**. North America, middle or late Cambrian.

Moths see **Lepidoptera**.

Moythomasia a basal genus of small palaeoniscoid actinopterygian fish. Only 4 inches long, *Moythomasia* had a downward-pointing tail with a row of bony nodes along its dorsal edge. Like the much larger *Cheirolepis*, it had overlapping ganoid scales connected in a peg and socket design. Europe and Australia, Middle to Late Devonian.

MRCA an acronym for “most recent common ancestor”; sometimes LCA (last) or “concestor.”

Mucrospirifer a well-known genus of rhynchonellate brachiopods in the order Spiriferida. *Mucrospirifer* was 1–2 inches long and had a very wide hinge line and a prominent fold and sulcus. Several species are index fossils for the Middle and Late Devonian. Asia, North and South America, and Europe; Early Devonian to Middle Mississippian.

Müllerian mimicry see **Batesian mimicry.**

Multituberculata a large and very successful order of early mammals, classified separately from the Theria and the Monotremata but closer to the Theria. Omnivorous but generally herbivorous, the rodent-like multituberculates include the earliest herbivorous mammals. Generally distinguished by large incisors and two or three longitudinal rows of simple conical cusps, there are many families, ranging in size from a few inches to 4 feet long. Global distribution but principally in the northern continents, Late Jurassic to late Eocene or early Oligocene.

Murchisonia a long-lived genus of prosobranch gastropod mollusks in the family Murchisoniidae. Characterized by a

2 inch, elongated, and high-spired shell, *Murchisonia* generally had rounded whorls with a deep-slit band that runs in a spiral ridge from bottom to top. Global distribution, Early Ordovician to Late Triassic.

Murgon fossil site a site in Queensland that has produced the Tingamarra fauna, a great diversity of fossils from the early Eocene. Among its important discoveries is *Djarthia*, the earliest-known marsupial of Australia, and another is ***Alamitophis tingamarra***, *q.v.*, a partial skeleton of a snake known also from Argentina. Australia, early Eocene.

Muridae a family of small mammals including mice, rats, and gerbils. Stem murids appeared in the early Eocene, probably sharing the ancestry of the Dipodidae, and true murids enter the fossil record in the early Miocene. The murids are the largest mammal family, diversifying from the middle Miocene to the Pliocene, and since the Pleistocene thriving commensally with humans. Global distribution, early Eocene to Recent.

Muscle scars roughened places on bones where muscles were attached.

Mustela vison see ***Neovison***.

Mustelidae a large extant family of caniform carnivorous mammals in the superfamily Musteloidea. The family includes the ancestors of modern weasels, martens, otters, badgers, minks, ferrets, wolverines, fishers, and stoats. Like other Carnivora, the first mustelids probably descended from the Miacidae in the Eocene; the earliest fossil specimens, however, date from the end of the Oligocene. Global distribution, Oligocene to Recent.

Muttaburrasaurus a genus of ornithischian dinosaurs in the iguanodont family Rhabdodontidae. Herbivorous, up to 26 feet long, and weighing 3 tons, it had significant forelimbs but was probably mainly bipedal. See also ***Altirhinus*****.** Australia, Early Cretaceous, 112–100 Ma.

Myalinidae a family of deep infaunal bivalve mollusks in the order Myalinida and superfamily Ambonychioidea. Both marine and freshwater genera are important

stratigraphically, especially in the Carboniferous. See also ***Naiadites***. Global distribution, Ordovician to Triassic.

Myanmarpithecus a proposed genus of primates in the family Amphipithecidae, found in 2001 in the Pondaung Hills of Burma; Eocene.

Myelodactylus a genus of unusual crinoids in the superorder Disparida and superfamily Myelodactyloidea. Probably free-living, perhaps lying on the substrate, *Myelodactylus* is especially distinguished by long, coiling arms with cirri on the inside. North America and Europe, early Silurian to Late Devonian.

Mygalomorphae an extant clade of spiders in the suborder Opisthothelae. It includes the tarantulas and the funnel and trapdoor spiders. Mygalomorphs are characterized especially by fangs that are parallel, pointing straight down, and also by their longevity, commonly living for two decades. Mygalomorph fossils go back at least as early as *Rosamygale* of the Early Triassic. Cosmopolitan, Early Triassic to Recent.

Mylagaulidae a family of sciuromorph rodents which includes the horned rodent *Ceratogaulus*; possibly related to the Aplodontiidae. North America and Asia, late Oligocene to early Pliocene.

Myledaphus bipartitus a species of freshwater guitarfish, rays in the extant family Rhinobatidae. Cartilaginous and known almost solely from teeth and vertebrae, it is estimated to have been 3 feet long. Since its broad, usually hexagonal, teeth are well-adapted for durophagy, *Myledaphus* probably depended on shellfish for its primary diet. Canada, the United States, and Uzbekistan; Late Cretaceous.

Myllokunmingia a genus of basal chordates in the family Myllokunmingiidae, generally considered the earliest-known vertebrate. About an inch long, it had a notochord and a skull and skeletal structures made of cartilage. China, early Cambrian, 530–525 Ma.

Mylodon see ***Paramylodon***.

Myodocopa one of the two subclasses of ostracods. Less well-known than the Podocopa because of weaker shell calcification, myodocopans are a problematic group. They are all marine except for the Leperditicopida (both freshwater and marine), which may be myodocopans or a separate subclass. The two accepted myodocopan orders are the Myodocopida and Halocyprida. Rare details of internal anatomy are revealed in "virtual" specimens (from the Herefordshire Nodules) of the family Cylindroleberididae. Global distribution, Middle Ordovician to Recent.

Myodocopida one of the two accepted orders of ostracods in the subclass Myodocopa. They are identified generally by a rostrum under which the antennae extend, and by lateral compound eyes. Global distribution, at least from the Silurian to Recent.

Myohyrax see **Macroscelidea**.

Myomorpha an extant suborder of mouse-like rodents. It includes mice, rats, lemmings, voles, and others, mainly in the superfamily Murioidea. Global distribution, early Eocene to Recent.

Myophorella a genus of marine bivalve mollusks in the order Trigoniida and extinct subfamily Myophorellinae. The irregularly shaped shell is covered with rows of tubercles, and in some specimens the soft tissue has been mineralized and preserved. Global distribution, Early Jurassic to Early Cretaceous.

Myotragus balearicus a species of bovid mammals in the subfamily Caprinae. Although commonly referred to as "mouse goat" or "pygmy goat," it is more closely related to sheep than to goats. Only 20 inches high at the shoulder, it is a clear example of island dwarfism. Known only from the Balearic Islands, Majorca and Minorca; early Pleistocene to Holocene, about 5000 years ago.

Myriapoda a subphylum of arthropods that includes centipedes, millipedes, arthropleurids, and other small groups; global distribution, Cambrian to Recent.

Mysticeti the baleen whales, a suborder of generally toothless, filter-feeding cetaceans that appeared at the end of the Eocene or beginning of the Oligocene. The modern Mysticeti include fin, gray, humpback, right, and blue whales, the latter at 110 feet being the largest animal known to have existed. They evolved from an archaeocete ancestor, probably separately from the odontocetes. Some early genera were partially toothed, and the evolution of fully edentulous baleen whales is well-documented in the fossil record. The North Pacific family Aetiocetidae of the early Oligocene was toothed but also had baleen structures in the jaw. The South Pacific family Mammalodontidae of the late Oligocene, including *Mammalodon* and *Janjucetus*, consists of early toothed mysticetes, some of them having a dentition similar to that of their terrestrial ancestors. The family Aetiocetidae contains genera (e.g., *Aetiocetus* and *Chonecetus*) of stem mysticetes with both teeth and baleen. See also ***Llanocetus***. The size of baleen whales stayed relatively constant through the Miocene but increased rapidly in the Pliocene for unknown reasons. Late Eocene to Recent.

N

Nacholapithecus a genus of hominoids dated at 15 Ma and tentatively placed in the family Proconsulidae. *Nacholapithecus* is known from a partial skeleton, the most complete specimen of a Miocene ape. Kenya, middle Miocene.

Nacimiento Formation a lower Paleocene heterogeneous nonmarine formation in western New Mexico, composed of sandstone, shale, and siltstone. Laid down primarily in lacustrine and floodplain environments, it has produced many fossils from the time after the end-Cretaceous extinction, including *Champsosaurus*, taeniolabidoids, and the early primate *Torrejonia*. United States, 65–61 Ma.

Naegele's giant jaguar see ***Panthera leo atrox***.

Nahecaris a genus of malacostracan crustaceans in the subclass Phyllocarida. About 6 inches long, it has long antennae, a pointed tail, and several pairs of short legs. Germany and Morocco, Early Devonian.

Naiadites a genus of nonmarine bivalve mollusks in the family Myalinidae. Along with *Carbonicola* and *Anthraconaia*, it is an index fossil in the British Coal Measures of the Carboniferous. Cosmopolitan, Late Mississippian to Early Pennsylvanian.

Najash a monospecific genus of early terrestrial snakes in the clade Ophidia. Known from a partial skeleton, *N. rionegrina* is significant for still having hindlimbs. Argentina, Cretaceous, 99–95 Ma.

Nalacetus ratimitus a species of archaeocete mammals in the family Pakicetidae. One of the earliest cetaceans, it is known from partial jaw and dental remains and estimated to be wolf-sized, probably larger than *Ichthyolestes* and about the same size as *Pakicetus*. Pakistan, Eocene, 50 Ma.

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Namacalathus a genus of enigmatic organisms that are among the earliest organisms to secrete a calcareous shell. It was a stalk with a cup at one end, with holes in the cup; the stalk was less than an inch long. See also ***Cloudina*** and ***Namapoikia***. Best known from Namibia, it may be known also from Canada, Russia, and Oman; late Ediacaran, 550–542 Ma.

Nama Group rock formations in Namibia that have produced three-dimensional casts of Ediacaran and very early Cambrian organisms. See ***Swartpuntia***. 570–543 Ma.

Namapoikia rietoogensis a species of enigmatic organisms among the earliest to secrete a calcareous shell. Up to 3 feet in diameter, it is vaguely coral-shaped. See also ***Cloudina*** and ***Namacalathus***. Known only from Namibia, late Ediacaran, 550–542 Ma.

Nannippus "dwarf horse," a genus of perissodactyl mammals in the family Equidae. It appeared in the late Miocene and coexisted with other North American horses until it became extinct in the late Pliocene. It was small and slender, the largest species as tall as a Shetland pony and resembling a gazelle. Differing from most other horses, it had three toes on each foot. North America and Eurasia.

Nanoparia a genus of procolophonomorph reptiles in the family Pareiasauridae. About 2 feet long, it was armored with many spines and scutes and, although poorly known, is considered a dwarf pareiasaur. South Africa, late Permian.

Nanosaurus see ***Othnielosaurus***.

"Nanotyrannus" a possible genus of dinosaurs similar to *Tyrannosaurus rex* but smaller and slightly different in other features. The four examples are generally considered to be simply juvenile specimens of *T. rex*, but examination of the skeletons has been inconclusive. The latest to be found (in 2013) is up for sale in 2019 and has not yet been carefully studied. North America, Late Cretaceous.

Naracoorte a cave site in South Australia that has produced well-preserved fossils from the middle to end of the Pleistocene.

Naraoia a genus of unusual trilobite-like arthropods in the order Nektaspida and family Naraoiidae. From 1 to 2 inches long, *Naraoia* had a soft exoskeleton and no thoracic segments, only the cephalon and a thoracopygidium twice as long as the cephalon. First discovered in the Burgess Shale, it was initially thought to be a crustacean and later classified as a trilobite. North America, Asia, and Australia; early Cambrian to late Silurian.

Nassellaria an order of marine protists in the subclass Radiolaria. Their siliceous skeletons are circular and generally have spiky pseudopods. The Nassellaria are

important stratigraphically where calcareous skeletons have dissolved. Global distribution, Miocene to Recent.

Nasutoceratops titusi a species of midsized North American ceratopsid dinosaurs in the subfamily Centrosaurinae. Dated at 75 Ma and known only from a partial skeleton, *N. titusi* is considered a basal centrosaurine. It has a pair of curved, forward-facing horns, a large nose, and a skull 5–6 feet long. Kaiparowits Formation, Utah; Late Cretaceous.

Natica a genus of predatory marine gastropod mollusks in the clade Littorinimorpha and family Naticidae, commonly called moon snails. Small- to medium-sized, *Natica* was low-spired and up to 2 inches high, with smooth whorls and a bulbous final whorl with a large aperture. Global distribution, Devonian to Recent.

Natural selection the basic nonrandom process by which evolution occurs, combined with small random genetic variations in individual organisms. Darwin, in his formulation of the process of natural selection, said that species improve through the accumulation of many small inherited variations, each of which gives the individual possessing that variation an advantage in the competition, among all the members of the species, for the necessities of life. Natural selection thus preserves those variants or traits best adapted to flourish. The offspring of these individuals will, over some period of time, outnumber disadvantaged individuals and become a new species. See also **modern synthesis**, **punctuated equilibrium**, and **typostrophism**.

Nautiloidea an important, extant subclass of externally shelled marine cephalopod mollusks that first appeared in the late Cambrian and flourished in the Ordovician. Nautiloids were the earliest large group of chambered cephalopods. The chambers were separated by septa, through which a tube called a siphuncle passed to move water from one chamber to another. Most early nautiloids, such as *Orthoceras* and *Ellesmeroceras*, are orthoconic (straight-shelled), but curved and coiled shells also appeared early; the Tarphycerida of the Early Ordovician were the first of the coiled cephalopods, which became more numerous in the Devonian and Carboniferous. Orthoconic species declined in the Triassic and disappeared early in the Cretaceous.

The nautiloids are ancestral to the Ammonoidea, which appeared in the Early Devonian and also diversified rapidly. Nautiloids declined somewhat through the Paleozoic (probably through competition with their close relatives the ammonoids and coleoids), but they continued to diversify. Most became extinct at the end of the Permian, but the order Nautilida persisted, although in decreasing numbers after the Miocene; it is still represented by two genera, *Nautilus* and *Allonautilus*. For an early nautiloid, see ***Plectronoceras***.

Neandertal the name of the valley in northwestern Germany where the first Neanderthal skeleton was found in 1856.

Neanderthal the common name of a group of hominins who lived in Europe, Africa, and Asia in the late Pleistocene from more than 300,000 years ago to about 30,000 years ago. They are now classified either as a separate species, *Homo neanderthalensis*, or as a subspecies, *Homo sapiens neanderthalensis*. The Neanderthals were less dimorphic and somewhat shorter and heavier-set than modern humans and were distinguished by a prominent brow ridge, a receding chin, and a slightly larger cranial capacity (1450 cc) than the modern average.

Nectridea an order of aquatic amphibians in the extinct subclass Lepospondyli. Generally resembling large newts, the largest nectrideans grew to 3 feet long. They are distinguished by large protrusions on either side of their flattened skull, which resembles a thick boomerang. The United States, Europe, and Africa; Late Carboniferous to Permian.

Necrolestidae a monogeneric family of small pantothere metatherian mammals. The insectivorous *Necrolestes* seems to be unrelated to any modern animal. Argentina, early Miocene.

Necrosis see **taphonomy**.

Neeyambaspis enigmatica see ***Pituriaspis***.

Nektaspida an order of trilobite-like arthropods, generally considered to include the Naraoiidae and Liwiidae; Africa, North America, Europe, and Asia; Cambrian to Silurian.

Nektic referring to organisms that live in the water column, swimming actively in open water and able to move independently of water currents, as opposed to plankton, which drift with the current; see also **pelagic, planktic,** and **benthic**.

Nektobenthic swimming freely but just above the bottom.

Nemagraptus a genus of early graptoloids in the family Nemagraptidae. It is distinguished by multiramous S-shaped, reclined stipes. Cosmopolitan, Middle to Late Ordovician.

Nemagraptus gracilis a species of *Nemagraptus* whose first appearance marks the beginning of the Late Ordovician at 458.4 Ma; Sweden.

Nematophyta a poorly known group of plants with characteristics of both vascular plants and algae. Sometimes classified as a phylum containing the type genus *Nematothallus* and four other genera. North America and Europe, Silurian to Early Devonian.

Nemegtosauridae a family of titanosaurian saurischian dinosaurs in the order Sauropodomorpha. Its classification is disputed, but it may be related to *Rapetosaurus* and *Saltasaurus*. Mongolia, Early to Late Cretaceous.

Nemertea an extant phylum of carnivorous ribbon worms, usually marine but some terrestrial; synonym Rhynchocoela. They are narrow and usually from 1 to 7 inches long, but some are much longer. Global distribution, Jurassic to Recent.

Nemicolopterus crypticus a contentious species of small, toothless pterosaurs in the suborder Pterodactyloidea, possibly related to the Tapejaridae. It had curved toes, indicating that it was essentially a tree-dweller. Probably insectivorous, it lived in a forested area of Western China around 120 Ma, whereas most previously known pterosaurs have been found in coastal environments. It may be a hatchling or juvenile, but if it is an adult, it is one of the smallest known pterosaurs, since the holotype is the size of a sparrow. China, Early Cretaceous.

Neocathartes see **Bathornithidae**.

Neodiapsida a clade of reptiles that includes later diapsids, excluding the Araeoscelida and some other primitive groups.

Neogene the second period of the Cenozoic Era, including the Miocene and Pliocene Epochs.

Neognathae the larger of the two groups of living birds, dating back to about 100 Ma and including all living birds except the Palaeognathae (the flightless ratites and the tinamous). Despite their name, they are believed to have appeared earlier than the Palaeognathae. Early Cretaceous to Recent.

Neoproterozoic the most recent era of the Precambrian Eon, from 1000 to 541 Ma. See also **Geologic Time Scale**.

Neoptera a major taxonomic group of insects in the subclass **Pterygota**, *q.v.* The Neoptera includes almost all of the flying insects, specifically those that can flex their wings back over their abdomen. Global distribution, Late Carboniferous to Recent.

Neosolenopora see ***Solenopora***.

Neospirifer a genus of articulate brachiopods in the family Trigonotretidae. Its wide spiriferid hinge line was up to 2 inches across, and *Neospirifer* is characterized also by robust, biconvex valves and a prominent sulcus and fold. Several genera are important stratigraphically. Global distribution, Early Carboniferous to late Permian.

Neosuchia a large and very diverse clade of crocodylomorphs that includes the extant crocodiles and their relatives as far back as the Early Jurassic.

Neotamandua see **Pilosa**.

Neotype a type specimen selected as a replacement holotype when the original has been lost or destroyed.

Neovison macrodon the sea mink, a small, marginally marine mustelid mammal in the subfamily Mustelinae. One of several formerly terrestrial mammals that have evolved into a saltwater habitat, it was formerly called *Mustela lutreola* and *Mustela vison*. It bore a pelt that was 30 inches long when processed, much larger and bulkier than that of the terrestrial species. *Neovison* lived in coastal waters off northeastern North America and was thus not truly marine. Since its remains date back only about 5000 years, it was probably a recently differentiated species. However, it is poorly known because of being hunted to extinction in the mid-nineteenth century before it could be studied thoroughly.

Nephila an extant genus of orb-weaver spiders in the order Araneae and family Nephilidae. Modern nephilids are the largest web-weaving spiders, with a body length up to 2 inches and leg span up to 6 inches; their webs may reach 5 feet wide. Although the fossil record is sparse, *Nephila* is known from several Miocene amber specimens and one Eocene specimen (*N. pennatipes*, from the Florissant Fossil Beds). An Indian specimen reported in 2019 has also been tentatively referred to the genus. See also ***Mongolarachne*.**

Nerinea a high-spired genus of marine gastropod mollusks in the family Nerineidae. Its slender, straight-sided shell grew to 5 inches long, with a notch at the aperture. Global distribution, Jurassic and Cretaceous.

Nesophontes the only genus in the extinct soricomorph family Nesophontidae. Commonly called West Indies shrews, these small insectivorous mammals may have survived until the early twentieth century. They may be related to the extant Solenodontidae of Cuba and Haiti. Known only from the Caribbean, late Pleistocene to Holocene.

Neurankylus a genus of baenid turtles widespread in western North America in the Cretaceous. Possibly related to the moderate-sized *Compsemys* of the Paleocene, *Neurankylus* was a freshwater turtle, with an extra pair of ribs but only nine vertebrae. North America and Asia, Late Cretaceous to Paleocene.

Neuroptera an extant order of pterygote insects in the clade Neuropterida. Including the lacewings, ant lions, mantidflies, and owl-flies, the neuropterans have four large wings, all generally of the same size; the membranous wings have exten-

sive patterns of venation and cross-venation. The Neuroptera are especially well-known from the Early Cretaceous Crato Lagerstätte of Brazil. Global distribution, early Permian to Recent.

Neuropterida a clade of pterygote insects that includes the extant orders Neuroptera, Megaloptera (alderflies, dobsonflies, and fishflies), and Raphidioptera (snake flies). Recognizable from the netlike venation in their large wings, members of the clade are known from the early Permian. Global distribution, Permian to Recent.

New Zealand avifauna see ***Harpagornis***.

Ngandong fauna a fossil assemblage containing the remains of several hominins found between 1931 and 1933 at Ngandong, Java, commonly referred to as the "Solo Man" fossils. The site is about 100 km from similar sites at Jetis and Trinil, the site of the "Java Man" find. With a cranial capacity range of 1035–1255 cc, Solo Man may represent a transitional stage between *Homo erectus* and *H. sapiens*. Indonesia, late Pleistocene, between 500,000 and 140,000 years ago.

Niche partitioning structural or behavioral differentiation between species competing for the same resources; synonyms niche differentiation, niche diversification. Such divergence results from a variety of causes, with availability of different food resources being the most common. See also **adaptive radiation**.

Nilpena see **Ediacara Conservation Park**.

Nilssoniopteris a form genus of leaves from cycad-like plants in the order Bennettitales; its taxonomy is disputed. United States, Europe, and Asia; Triassic to Cretaceous.

Nimravidae a family of carnivorous mammals in the suborder Feliformia. Catlike but not true cats like *Smilodon* or the earlier machairodonts; they had several nonfelid traits, including nonretractable claws and skeletal differences. North America, Europe, and Asia; middle to late Miocene.

Nimravides a genus of machairodont mammals in the family Felidae. Up to 6 feet long and about 220 pounds, it was a true saber-toothed cat. North America, middle to late Miocene.

Nimravus a genus of small saber-toothed mammals in the family Nimravidae. Catlike but not a true felid, *Nimravus* was 4 feet long and probably weighed less than 70 pounds. Western North America, early to middle Oligocene.

Niobrara Sea see **Western Interior Seaway**.

Nipponites a genus of heteromorph ammonoids in the suborder Ancyloceratina and family **Nostoceratidae**, *q.v.* Famous for a very unusual shell form, *Nipponites* resembles a tangle of knots. The tubular shell reaches lengths of almost 2 feet if extended and might reach a diameter of 10 inches if coiled planispirally in the normal ammonoid manner. But it coils on itself on different axes, creating a globular shape only 3–4 inches in diameter. Japan, Asia, United States, and possibly Madagascar; Late Cretaceous.

Nodosauridae a large family of ornithischian dinosaurs in the suborder Ankylosauria. Herbivorous, squat, and quadrupedal, they grew as long as 20 feet. Nodosaurs were heavily armored, generally with large shoulder spikes, but without a tail club. Well-known in the genus ***Borealopelta***, *q.v.* North America, Europe, Asia, and Antarctica; Late Jurassic to Late Cretaceous.

Noeggerathiales an unusual order of fernlike vascular plants in the division Tracheophyta and extinct class Progymnospermopsida. The Noeggerathiales have some similarities to modern conifers and araucarians, but they may have reproduced by spores. There was a notable 2012 discovery of a specimen in a large (20 square km) forest buried in Lower Permian volcanic ash in China. But because of gaps in their fossil record, the Noeggerathiales are still poorly known, and they may be related to either the Equisetopsida or the Pteropsida. North America, Europe, and Asia; Late Devonian to Late Triassic.

Noguerornis one of the earliest-known enantiornithean birds, a poorly known specimen from the beginning of the Cretaceous. *Noguerornis* was much smaller than *Archaeopteryx* and more capable of flight. El Montsec, Spain, Early Cretaceous, 130–125 Ma.

Nomen dubium plural nomina dubia; a name of unknown or doubtful application, often referring to a lost type specimen.

Nostoceratidae a diverse family of heteromorph ammonoids in the suborder Ancyloceratina and superfamily Turrilitoidea. Most genera coil in unusual directions, sometimes partly planispirally. *Nipponites* resembles a randomly coiling knot, while the tubular *Bostrychoceras and* the type genus *Nostoceras* create a helical spire shape. Global distribution, Late Cretaceous.

Nostolepis a genus of acanthodian fish in the order Climatiiformes and family Climatiidae. About 4 inches long, with pairs of spines, and head and body covered with distinctive scales. Canada, Europe, Asia, and New Zealand; late Silurian to Early Devonian.

Notharctus a genus of adapiform primates of North America, related to *Smilodectes* and possibly the Amphipithecidae. The lemur-like *Notharctus* is an example of the

evolutionary trend in primates toward greater brain size, reduction of muzzle size, and the capability for stereoscopic vision – cephalic hallmarks of advanced primates and of humans. Early to middle Eocene.

Notharctus tenebrosus a species of *Notharctus* found first in Wyoming in 1870. It was evidently adapted to a fine-branch niche in its arboreal habitat, having long fingers, an opposable thumb, and nails instead of claws. North America, middle Eocene, 50 Ma.

Nothosauroidea an order of seallike aquatic sauropterygian reptiles with two suborders, Nothosauria and Pachypleurosauria. From 8 to 13 feet long, the nothosaurs evolved from the much smaller pachypleurosaurs, which were mostly 1–3 feet long. They were related to but probably not directly ancestral to the plesiosaurs, which replaced them at the end of the Triassic (see **Pistosauria**). North America, Europe, Asia, and Africa; Early to Late Triassic.

Nothrotheriidae a family of ground sloths in the order Pilosa. Related to the larger Megatheriidae, they migrated to North America at the beginning of the Pleistocene as part of the Great American Biotic Interchange. South and North America, late Miocene to 11,000 years ago.

Nothrotheriops shastensis the Shasta ground sloth, a species of giant sloth in the family Nothrotheriidae. It appeared at the beginning of the Pleistocene and became extinct about 11,000 years ago. Known from Mexico to Oregon and especially abundant in the La Brea Tar Pits; western North America, Pleistocene.

Notiomastodontinae a subfamily of proboscideans in the extinct suborder Euelephantoidea and family Gomphotheriidae; South America, late Pleistocene.

Notioprogonia a probably paraphyletic suborder of primitive mammals in the extinct order Notoungulata, with a more primitive dentition than that of any other notoungulate. From 3 to 5 feet long, some genera resembled rabbits in appearance. Two families are currently recognized, the Henricosborniidae and the Notostylopidae. South America, Paleocene to Eocene.

Notochord a stiff, flexible dorsal rod, the main identifying character of chordates. The notochord is the developmental and evolutionary precursor of the vertebrate backbone.

Notocupoides a genus of coleopteran insects in the family Ommatidae. From 4 to 5 inches long, it is known only from the Madygen Formation. Kyrgyzstan, Late Triassic, 230–225 Ma.

Notoryctidae an extant family of marsupial moles in the order Notoryctemorphia. They have no external ears, and their eyes are vestigial lenses under the skin. They are poorly understood but are possibly related to the Miocene mole *Yalkaparidon coheni*. Australia, Miocene? to Recent.

Notosuchus a genus of crocodylomorph reptiles in the order Notosuchia. About 3 feet long and 80 pounds, *Notosuchus* preyed on small animals. Poorly known and restricted to the Coniacian and Santonian Ages, 90–84 Ma; South America, Late Cretaceous.

Notoungulata a large order of generally hoofed mammals in the superorder Meridiungulata. Like all ungulates, they were basically herbivorous, with some omnivorous. Some genera, such as *Mixotoxodon* and *Toxodon*, were quite large, but others filled the same ecological niches as rabbits and hyraxes. Basically South American, but some genera (see ***Mixotoxodon***) are found as far north as the southern United States. Paleocene to 11,000 years ago.

Nucleolitidae a family of generally atelostomate echinoids in the superorder Microstomata. The most primitive genus is *Pronucleolites*. The traditionally recognized group is probably paraphyletic, and some authorities treat the family as only Mesozoic (Jurassic to Cretaceous). North and South America, Europe, Africa, and Asia; Middle Jurassic to middle Pleistocene.

Nucula a genus of articulate marine bivalves in the order Nuculoida and family Nuculidae. Almost unchanged since the Silurian, it is an inch long, subtriangular, and symmetrical, with many small teeth and sockets on both sides of the hinge. Global distribution, Early Ordovician to Recent.

Nummulitidae a family of large foraminiferans in the order Rotaliida. Lenticular and from half an inch to 4 inches in diameter, nummulites are named for their coin shape. Distinguished by narrow, helical coils of septa, they are found principally in shallow-water deposits of the Paleogene, but they still exist in some tropical areas. They appear in the limestone used for the Egyptian pyramids and were probably used as jewelry and coins in Egypt. Cosmopolitan, Early Cretaceous to Recent.

Nuna see **Rodinia**.

Nuttalliellidae a monotypic family of ticks in the order Ixodida. Genetically identified as the most basal lineage of ticks, the family contains one species, *Nuttalliella namaqua*. It is estimated to be more than 200 million years old, but no fossil specimens have been identified. See also **Ixodida**.

Nyasasaurus a genus of early dinosauriform reptiles that may be the earliest-known dinosaurs. The type species, *N. parringtoni*, was 10 feet long and is dated at 243 Ma, about 12 million years earlier than any other of the oldest dinosaurs known (see ***Eoraptor***, ***Herrerasaurus***, and ***Staurikosaurus***). Described in 2013 but poorly known, its placement is disputed; research in 2017, however, seems to support its identification as a dinosaur. Tanzania, Early Triassic**.**

Nyctitheriidae a family of soricomorph mammals. Scansorial insectivores, the family is generally considered eulipotyphlan (related to shrews, hedgehogs, and moles) but claimed by some as euarchontan (closer to tree shrews and primates). North America, Europe, Africa, and Asia; Late Cretaceous to early Miocene.

Nyctosaurus a genus of pterodactyloid pterosaurs, notable for a large crest supported by two antler-like spars 1–2 feet long. Smaller than its relative *Pteranodon*, its body was only a foot long, but *Nyctosaurus* had a wingspan of up to 7 feet. Known only from Kansas, United States; Late Cretaceous, 86–84 Ma.

Nymphaeales see ***Pluricarpellatia***.

O

Obamus coronatus a species of Ediacaran organisms described in 2018. About half an inch long, it is circular to oval, with a hole in the middle, probably a torus, and with twining ridges on the surface. It was probably embedded in a biofilm on the substrate. Flinders Ranges, Australia, 550 Ma.

Obligate necessary, by necessity; see also **facultative.**

Obolellata one of the four extinct classes of brachiopods in the subphylum Rhynchonelliformea. It is a small class, formerly labeled inarticulate but now considered primitively articulate. It contains only one order, Obolellida. Cosmopolitan, early to middle Cambrian.

Obolellida "small coin," an order of rhynchonelliform brachiopods in the class Obolellata, distinguished by impunctate biconvex shells and at first inarticulate. Among the earliest brachiopods, they were a short-lived but widespread order that began to exhibit some articulation in the later genera. They are considered part of the Tommotian biota, the early Cambrian wave of evolution of invertebrate animals that included the archaeocyathans, trilobites, and echinoderms. Cosmopolitan, early to middle Cambrian.

Obovothyris a genus of terebratulid brachiopods in the family Zeilleriidae, with a long loop and a biconvex, punctate shell; Europe, Middle Jurassic.

Ocepeia a genus of small, primitive mammals, incertae sedis but placed tentatively in the clade Paenungulata. Known from several skull fragments (possibly of two species), it was a cat-sized herbivore of 8–22 pounds. Morocco, middle Paleocene.

Octocorallia a subclass of anthozoan cnidarians including the soft corals and sea pens. They were generally colonial polyps without a calcareous or aragonitic skeleton. Cosmopolitan, Cambrian to Recent.

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Odaxosaurus a genus of squamates in the family Anguidae and subfamily Glyptosaurinae, widespread in at least two species across North America in the Late Cretaceous. One species, *O. piger*, was one of the few lizards that survived the end-Cretaceous extinction. North America, Late Cretaceous to late Paleocene.

Odobenidae the walruses, a family of carnivorous pinnipeds in the superfamily Otarioidea. At least 24 extinct species of walrus are known, evolving from bearlike land animals of the late Oligocene, with only one species still surviving. See also ***Enaliarctos***.

Odobenocetops peruvianus a species of monodontid whales in the superfamily Delphinoidea, known only from the Pacific coast of South America. Related to the narwhal, Odobenocetops grew as long as 7 feet, had a blunt snout and two short tusks, and seems to have been a bottom feeder with walrus-like features. Chile and Peru, late Miocene to early Pliocene.

Odonata an order of carnivorous pterygote insects that includes the dragonflies (Anisoptera) and damselflies (Zygoptera). The earliest odonatans include the giant *Meganisoptera* of the Carboniferous and Permian. They were traditionally grouped with mayflies and several extinct groups in the paraphyletic classification Palaeoptera. Global distribution, Triassic to Recent.

Odontoceti a suborder of toothed whales, including the modern orcas, sperm whales, beaked whales, dolphins, and porpoises. The early odontocetes appeared in the late Eocene, the Agorophiidae being the most primitive. The Oligocene superfamily Squalodontoidea may be ancestral to most modern odontocetes. Global distribution, late Eocene to Recent.

Odontochelys semitestacea "half-shelled turtle with teeth," an early genus of stem-turtles in the family Odontochelyidae. Its three specimens were found in marine deposits, but it is thought to have been partly terrestrial. It was about 16 inches long and had teeth in both jaws, with a plastron covering its belly but only broad ribs and the knobby rudiments of a carapace on its back. Guizhou Province, China, Late Triassic, 237–233 Ma.

Odontognathae an obsolete term for a paraphyletic group of primitive toothed birds of the Cretaceous, similar to modern birds in having a pygostyle. Current classifications have placed the group in the large clade Ornithurae. North and South America, Cretaceous.

Odontogriphus omalus a species of soft-bodied bilaterian mollusks in the family Odontogriphidae. The oldest mollusk known, prominent in the Burgess Shale, it continues to figure in current debates about the origins of mollusks, brachiopods, and annelids. *Odontogriphus* has an ovoid, shell-less body between 5 and 8 inches long, with simple gill-like structures surrounding the bottom of the foot on the

underside. Its stomach, intestines, outer membrane, and mouth are also visible in the specimens; a radula may also be visible. Canada, middle Cambrian, 508 Ma.

Odontopleurida an early order of trilobites related to the order Lichida. Odontopleurids were spinose, with especially long spines extending from the small pygidium. Global distribution, middle Cambrian to Late Devonian.

Oepikellidae a family of paleocopid ostracods in the suborder Beyrichicopina that generally had biconvex shells without a sulcus; global distribution, Ordovician to Devonian.

Oesia a genus of wormlike organisms considered a putative hemichordate. About 4 inches long, *Oesia* lived in tubes that were first thought to be seaweed. It is known only from the two Burgess Shale sites. Canada, middle Cambrian.

Ogygiocarella a small genus of trilobites in the family Asaphidae. Famous as a supposed "flatfish" discovery, it was described in 1698 by Edward Llwyd. It was slightly more than an inch in length, isopygous, flattened, and oval in shape. Wales and South America, Middle Ordovician.

Ogygopsis a genus of trilobites in the order Corynexochida and family Dorypygidae. Abundant in the Burgess Shale, *Ogygopsis* was a somewhat unusual trilobite. From 3 to 4 inches long and oval in outline, it has no pleural spines and 30 to 40 percent of its body length is in the large and rounded pygidium. North America, Antarctica, and Kazakhstan; middle to late Cambrian.

Öhningen site a locality on the German border with Switzerland; also spelled Oeningen. The site has produced many fossils from the Miocene, including the 3-foot-long salamander *Andrias scheuchzeri*, turtles, and many well-preserved flowers and insects. Germany, late Miocene.

Oldhamia a genus of ichnofossils consisting of deep marine worm burrows. Several species have long been used in early and middle Cambrian biostratigraphy. Research in 2010 indicates that the species *O. recta*, previously considered an Ediacaran ichnospecies, is actually a rodlike body fossil. *Oldhamia* is cosmopolitan but is known especially from Europe and the Americas. Cambrian, 540–505 Ma.

Olenellus a stratigraphically important genus of trilobites in the order Redlichiida and the only currently recognized genus in the subfamily Olenellinae. About 2 inches long, its features include a very large semicircular cephalon; a very spinose, elongated thorax; and a small pygidium with a telson. It is notable for its large, crescent-shaped eyes; species such as *O. transitans* had nearly 360-degree vision. North America, early Cambrian, in the Olenellus zone, 522–510 Ma.

Olenoides a genus of trilobites in the order Corynexochida and family Dorypygidae. It was up to 4 inches long and had small eyes, a raised glabella extending to the front of the cephalon, and many slender pygidial spines. More than 100 well-preserved specimens have been found in the Burgess Shale, including several with soft-tissue preservation. North America and Asia, middle to late Cambrian.

Olenus a genus of trilobites in the order Ptychopariida and family Olenidae. It is notable for 12 to 15 thoracic segments and pleurae with sharp recurved tips. An important index fossil, *Olenus* was widespread in the late Cambrian. The name comes from Olenus, a character in Greco-Roman mythology who was transformed into a stone pillar. Global distribution, late Cambrian.

Oligocene the third epoch of the Cenozoic Era, from 34 to 23 Ma. New genera of modern mammals were relatively rare, a fact reflected in the name, "time of few recent groups." However, several new groups did appear: the first barnacles, pigs, rats, and deer. The world climate continued to cool, causing fragmentation of marine populations and some extinctions. Early in the epoch, Antarctica began to be covered with ice, and the Grande Coupure in Eurasia caused several extinctions and large-scale rearrangement of biozones. Several large mammals became extinct, such as the brontotheres and embrithopods, but ungulates in general flourished and grew in size.

Oligopygoida a small order of irregular echinoids in the superorder Neognathostomata. They had a well-developed lantern and were closely related and possibly ancestral to the Clypeasteroida of the late Paleocene. Caribbean and Mexico, Eocene to Paleocene.

Olorotitan a genus of lambeosaurine dinosaurs in the family Hadrosauridae, closely related to *Corythosaurus*. About 26 feet long, it had a distinctive fan-shaped crest. It is known only from an almost complete specimen found in the Amur region of Eastern Russia. Late Cretaceous, 72–66 Ma.

Olsoniformes a clade of temnospondyl amphibians in the superfamily Dissorophoidea that includes the families Dissorophidae and Trematopidae. United States, Europe, and Asia; Late Carboniferous to middle Permian.

Olympicetus avitus a species of toothed whales, considered a stem odontocete. *Olympicetus* is known from two partial skulls found in the Pysht Formation on the Olympic Peninsula of Washington. Its nostrils are located in front of its eyes rather than behind the orbit as in later whales. It is also notable for multicuspate heterodont teeth, and it may have been able to echolocate. United States, early Oligocene, 31–27 Ma.

Omomyidae an important early family of tarsier-like primates in the suborder Haplorrhini and the infraorder Tarsiiformes. The family includes the earliest-known

crown primates and is probably ancestral to the modern tarsiers. North America, Europe, and Asia; early Eocene to early Miocene.

Oncorhynchus rastrosus the largest-known species of fish in the family Salmonidae. Known from two specimens from Central Oregon, it grew to about 9 feet long and weighed about 1000 pounds; it was probably anadromous like the modern salmon. The species is notable especially for the two 1-inch fangs protruding to the side like warthog tusks. United States, Miocene to Pleistocene.

Ontogeny the growth and development of individual organisms.

Onychaster a genus of brittle stars, ophiuroids in the family Onychasteridae; Europe and United States, Late Devonian to Early Carboniferous.

Onychodus "claw tooth," a genus of basal sarcopterygian fish in the family Onychodontidae, possibly related to *Psarolepis*. Poorly known but up to 12 feet long, *Onychodus* is especially notable for a pair of retractable tooth whorls at the anterior end of the jaw. Canada, Europe, and Australia; Middle to Late Devonian.

Onychonycteris finneyi a species of early bats, in the order Chiroptera and family Onychonycteridae. It is notable in having claws on all ten fingers. It probably could not echolocate, and it is taken as evidence that bats could fly efficiently before developing echolocation. It is considered the most primitive bat known although somewhat younger than *Icaronycteris*. See also **Chiroptera.** North America, late Eocene, 52.5 Ma.

Onychophora the "velvet worms," an extant phylum of small, caterpillar-like, predatory animals. The modern onychophorans are generally found in moist terrestrial habitats. Their fossil record is sparse, but they were an important and diverse group of marine invertebrates in the Cambrian. Paleozoic onychophorans are traditionally placed in their own class, the Xenusia; they were entirely marine and had a terminal mouth, as opposed to the ventral mouth of modern onychophorans. From the Burgess Shale assemblage, the famous *Hallucigenia* is considered an onychophoran, and *Aysheaia* is also thought to be related. The Carboniferous genus *Helenodora* is considered basal to modern onychophorans. See also ***Peripatus***. Global distribution, Cambrian to Recent.

Onychopterella a genus of chelicerate arthropods in the order Eurypterida and family Onychopterellidae. *Onychopterella* was relatively small, from 2 to 6 inches long; it had long walking legs, and in one species, the swimming legs end in a small claw. It has long been known from Silurian deposits in Indiana and Illinois, but the more recently discovered species (*O. augusti*) from the Soom Shale is especially well-preserved. United States and South Africa, Late Ordovician to late Silurian.

Oogonia see **charophyte**.

Oolitic "egg stone," a term usually referring to limestone formations consisting of calcium carbonate concretions that are similar in size and shape to fish eggs; see also **Great Oolite**.

Opabinia a stem arthropod genus of soft-bodied animals found only in the Burgess Shale and tentatively placed in the order Radiodonta. *Opabinia regalis*, the only known species, had a segmented body with lateral lobes, a fan-shaped tail, and a long and slender proboscis. Even less usual are its five eyes and a backward-facing mouth below the head. See also ***Jianfengia***. Canada, middle Cambrian, 508 Ma.

Opallionectes a species of Cretaceous plesiosaurs identified in 2006. It is known only from Central Australia, where it was found in company with the smaller plesiosaur *Umoonasaurus*. *Opallionectes* was 16 to 18 feet long and is notable for its large number of needlelike teeth adapted to trapping small fish and squid. Early Cretaceous, 115 Ma.

Operculum a structure in many animals, generally calcitic, whose function is usually to seal an aperture by opening and closing. It is a prominent feature in gastropods, ammonoids, and other cephalopods.

Opetiosaurus see **Aigialosauridae**.

Ophiacodon "snake tooth," a genus of primitive synapsid reptiles in the family Ophiacodontidae, close to the line of descent leading to mammals. About 10 feet long, it was much larger than earlier ophiacodontids and one of the largest early synapsids, with an unusually long snout containing more than 160 needlelike teeth. *Ophiacodon* was partly aquatic and similar to crocodiles in some ways although only distantly related and so an example of convergent evolution. United States and Europe, Late Pennsylvanian to early Permian.

Ophiderpeton an unusual genus of snakelike lepospondyl amphibians in the order Aïstopoda. From 2 to 3 feet long and very slender, it had 200 vertebrae in its spine and no limbs. It was mostly terrestrial and probably fossorial. United States and Europe, Early Carboniferous to early Permian.

Ophidia the snakes, a clade of squamate reptiles generally considered to include modern snakes (Serpentes) as well as proto-snakes such as *Najash*. Since the fossil record of snakes is sparse, their origins and classification are highly disputed. Global distribution, Early Cretaceous to Recent.

Ophiocistioidea a class of stemless echinozoan echinoderms. They are similar to modern sea urchins and are characterized by a flattened, dome-shaped test and five pairs of arms of varying length. Global distribution, Early Ordovician to Late Cretaceous.

Ophiopinna a genus of brittle stars, ophiuroids in the family Ophiacanthidae. About an inch across, hundreds of specimens are preserved at La Voulte-sur-Rhône, some with paddle-shaped spines, possibly an adaptation for swimming. France, Middle Jurassic.

Ophiurida an extant order of brittle stars, asterozoan echinoderms in the class Ophiuroidea. Global distribution, Devonian to Recent.

Ophiuroidea the brittle stars, a class of echinoderms in the extant subphylum Asterozoa, encompassing the brittle stars (Ophiurida) and basket stars (Euryalida). As in the sea stars (Asteroidea), the central body extends into five or more arms, but the ophiuroid body is sharply distinguished from the slender, very flexible arms, which are as much as 20 times longer than the diameter of the body. Also like the sea stars, brittle stars can move horizontally for locomotion. Since the ophiuroids disintegrate rapidly after death, complete skeletons are rare. Global distribution, Ordovician to Recent.

Ophthalmosaurus a genus of ichthyosaurian reptiles in the family Ophthalmosauridae. Named for its large eyes, which were 8–9 inches in diameter, it was toothless and viviparous, preying mainly on squid. North and South America and Europe, Late Jurassic, 165–160 Ma.

Opiliones the harvestmen, an extant order of arachnids noted for their very long legs. Although similar to spiders, they are not closely related. Harvestmen originated in the Devonian, the earliest known being *Eophalangium sheari* (Early Devonian, from the Rhynie chert). Global distribution, Devonian to Recent.

Opipeuterella a genus of nektic proetid trilobites in the family Telephinidae. It is remarkable for very large eyes that extend below the plane of the body, indicating that it was free-swimming rather than benthic. The thorax is slender and the pygidium ends in a spine. Cosmopolitan, Early to Middle Ordovician.

Opisthocomidae a family of large birds in the clade Ornithurae. It includes the modern hoatzin (*Opisthocomus hoazin*) of northern South America, which is a crested bird 28 inches long; it is herbivorous and is capable of flight but seldom does fly. Its chicks have two claws on each wing for the first 2 months of its life. Two extinct members of the family (*Hoazinoides magdalenae* of the Miocene in Colombia and *Hoazinavis lacustris* of the late Oligocene in Brazil) seem to show that the modern hoatzin's claws are a recent adaptation, not an inheritance from dinosaur ancestors. South America, Oligocene to Recent.

Opisthothelae an extant suborder of arachnids in the spider order Araneae, comprising almost all true spiders, including the clades Araneomorphae and Mygalomorphae. For differences from mesotheles, see **Mesothelae**. Global distribution, Carboniferous to Recent.

Opossum see **Didelphidae**.

Orbiculariae a suggested clade of araneomorph spiders.

Orbiculoidea a large genus of inarticulate brachiopods in the order Lingulida. Generally conical in shape, the species vary from half an inch to 2 inches in diameter, with a functional pedicle. Global distribution, Early Ordovician to Cretaceous.

Ordovician the second period of the Paleozoic Era, from 485 to 444 Ma, divided into Early, Middle, and Late Epochs. It was a time of high sea levels and marine transgressions, with a severe glaciation at the end of the period. During the Ordovician, the southern continent Gondwana coalesced and drifted south, and Laurentia, Baltica, and other land masses became separated from each other.

The first bony vertebrates appeared at the beginning of the Ordovician, including the first agnathans, the jawless fish; the first jawed fish are known from the middle of the period. Although vertebrates still appeared only in marine environments, there was greater overall ecological complexity than in the Cambrian.

Between 485 and 460 Ma, about 50 million years after the great radiation of life of the early Cambrian, marine life again experienced a rapid and extensive diversification. Although relatively few new invertebrate body plans appeared, the numbers of biological orders and families more than doubled, especially in brachiopods, bivalves, corals, crinoids, bryozoans, and gastropods. This development is referred to as the Great Ordovician Biodiversification Event (GOBE).

In the Middle Ordovician, localized faunas became established in different parts of the world, and many of these faunas remained relatively stable until the end-Permian extinction ended the Paleozoic Era. The first definitive terrestrial plants appeared near the end of the Early Ordovician, and, despite a lack of complete fossil specimens, there is some evidence of aquatic arthropods venturing into terrestrial environments.

Ordovician extinction the first of the five great extinctions, at the end of the Ordovician Period, about 444 Ma. More than 100 families of invertebrates and as many as 60 percent of marine genera became extinct, making it second in the number of extinctions only to the end-Permian extinction. As in the other mass extinctions of the Paleozoic, this one seems to have occurred in more than one pulse, in this case strongly associated with a major glaciational event at the beginning of the Hirnantian Age. The second pulse of extinctions occurred at the end of the Hirnantian (the end of the period), with no consensus as to its causes. This extinction, although extensive, had fewer long-term effects on life than some smaller extinctions that occurred later.

Oreodonts see **Merycoidodontidae**.

Oreopithecus "mountain ape," a genus of Miocene hominoids. *Oreopithecus* weighed between 60 and 80 pounds and had characteristics of hominids and of

dryopithecines; it may also be related to the parapithecines of the Oligocene. Known only from European and African sites of the late Miocene.

Ornithella a genus of articulate brachiopods in the order Terebratulida and family Zeilleriidae. Pentagonal in outline, *Ornithella* had an especially long loop. North America, Europe, and Asia; Middle Jurassic.

Ornithischia the "bird-hipped" dinosaurs, one of the two large orders. Almost all ornithischians are herbivorous, the principal groups being the ankylosaurs, ceratopsians, ornithopods, hadrosaurs, and stegosaurs; one family known to be omnivorous is the Heterodontosauridae. Ornithischians are identified first by a four-pronged arrangement of pelvic bones similar to that of birds. Another typical ornithischian trait is the predentary, a horn-covered beak-like structure at the front of the lower jaw bone that probably made it easier to crop vegetation. Although theropods and their descendants the birds have traditionally been considered saurischians, some classifications place them in the Ornithischia. Global distribution, Late Triassic to Late Cretaceous.

Ornithocheirus simus **"**bird hand," a species of pterodactyloid pterosaurs known only from fragmentary English specimens of the 1860s. It was medium-sized, with a wingspan of about 8 feet, and with a distinctive crest at the tip of its beak. Since the 1970s, several other species once assigned to *Ornithocheirus* have been reassigned or questioned. *Ornithocheirus simus* seems similar to Brazilian pterosaurs like *Anhanguera*, but its relationships are still unclear. England, Cretaceous, 110 Ma.

Ornithodira the clade that includes all avian archosaurs: dinosaurs and the Dinosauromorpha, pterosaurs, and birds; it is basically synonymous with the clade Avemetatarsalia.

Ornitholestes "bird thief," a monospecific genus of bipedal theropod dinosaurs, known only from an almost complete skeleton found at Como Bluff, Wyoming, in 1900. Lightly built and about 7 feet long, *O. hermanni* had long forelimbs and long, clawed fingers and preyed mainly on small mammals and lizards. United States, Late Jurassic, 154 Ma.

Ornithomimidae a family of coelurosaurian theropod dinosaurs. Up to 20 feet long and lightly built, with slim but strong hindlimbs, they were strong runners. Probably omnivorous, they had very large eyes but were toothless, with a slender skull and beak. Northern Hemisphere and possibly Australia, Late Cretaceous, 90–66 Ma.

Ornithomimosauria a clade of theropod dinosaurs that contains the basal *Harpymimus* and *Pelecanimimus*; several other groups such as the Deinocheiridae; and the more advanced Ornithomimidae. Slender and fast-running, they had strong

hindlimbs and a birdlike beak. Only the earliest had teeth, and they were generally omnivorous but mainly herbivorous. Northern Hemisphere, Africa, and possibly Australia; Early to Late Cretaceous, 140–66 Ma.

Ornithomimus a genus of birdlike theropod dinosaurs in the family Ornithomimidae. A fast runner, superficially similar to ostriches, *Ornithomimus* was 12–14 feet long but weighed less than 400 pounds. It had large eyes, hollow bones, and three toes and may have had feathers. The genus is best known from an articulated specimen of *O. edmontonicus* on display at the Royal Tyrrell Museum; it has part of the beak still attached to the jaws. Western North America, Late Cretaceous, 77–66 Ma.

Ornithopoda a suborder of medium to large herbivorous dinosaurs in the order Ornithischia. They include all of the bipedal ornithischians except the Pachycephalosauridae. The early ornithopods were small (3–10 feet long), and later ornithopods became semi-quadrupedal, the largest (such as the Iguanodontidae and Hadrosauridae) weighing as much as 25 tons. The ornithopods generally had three digits on birdlike feet, especially the later genera. Global distribution but rare in the Southern Hemisphere, Early Jurassic to Late Cretaceous.

Ornithorhynchus anatinus the platypus, one of the few living monotremes. Semiaquatic and egg-laying but a mammal, the modern platypus dates back to 100,000 years ago, closely related to monotremes of the Cretaceous. Found only in Eastern Australia, the adult is 1–2 feet long and toothless, but it possesses a poisonous spur on the hind foot. See also **Monotremata** and ***Steropodon***.

Ornithoscelida a term referring to groupings of dinosaurs that varied considerably over time. First proposed by T.H. Huxley in 1869 in his argument for seeing birds as descendants of dinosaurs, the term has been revived in a 2017 proposal for a large-scale revision of dinosaur classification. In this proposal the Ornithoscelida includes the Ornithischia and the Theropoda as sister groups, the Theropoda including the ancestors of birds.

Ornithurae a proposed term for all modern birds and their immediate ancestors, back to the common ancestor of *Ichthyornis* and *Hesperornis*. The basic feature of modern ornithurines is a short, fused pygostyle tail, as opposed to the longer, straight tails of primitive birds.

Orrorin tugenensis a controversial species of hominins found in the late 1990s in Kenya. It seems to be in the line of descent from chimpanzee to advanced hominins, possibly to humans, but is known only from fragments. Between 6.1 and 5.7 Ma, 1.5 million years earlier than similar hominins.

Orsten Konservat-Lagerstatten upper Cambrian deposits in Sweden, part of the Alum Shale Formation. The Orsten beds have yielded important fossils since the late twentieth century, especially of arthropod larvae and rare animals such as

pentastomes and tardigrades. The specimens are typically phosphatized and preserved inside calcareous nodules, so that when the nodules are dissolved, often a three-dimensional shell is left that preserves body structures in fine detail. Some of the Orsten fossils have no counterparts in the fossil record.

The recently discovered pentastomes, for example, are almost the only extinct pentastomes of which there is any record, and yet these fossil species are very similar to modern members of the phylum.

Orthoidea a superfamily of articulate rhynchonellate brachiopods in the suborder Orthidina, characterized generally by impunctate shells, an open delthyrium, and a functional pedicle. Global distribution, early Cambrian to the end of the Permian.

Orthida an order of articulate brachiopods in the class Rhynchonellata. They were generally strophic and between 1 and 2.5 inches in diameter. The Orthida, which include the earliest-known articulate brachiopods, arose early in the Cambrian and diversified widely into the Early Ordovician (the impunctate suborder Orthidina). The second of two suborders, the punctate Dalmanellidina, appeared in the Early Ordovician and is generally considered to have become extinct in the Permian. Global distribution, early Cambrian to middle Permian or possibly Triassic.

Orthoceras "straight horn," a genus, now considered monospecific, of nautiloid cephalopods in the order Orthocerida. The type species *O. regulare* was orthoconic: cone-shaped, thin, and about 6 inches long. The genus was long considered much longer-lived, extending from the late Cambrian to the Triassic, but most species have been reassigned. Orthocerids form Ordovician key beds in North America, Europe, and Africa. Similar to but not related to ***Baculites***, *q.v.* Global distribution, Early Ordovician to Early Devonian.

Orthocones cephalopods whose shell is an elongated, straight, tapering cone.

Orthogenesis an obsolete biological hypothesis that organisms have an innate tendency to evolve in a certain way determined by an internal driving force, rather than by external processes such as natural selection. Advanced in the early twentieth century, it was soon universally refuted and abandoned. See also ***Gryphaea***.

Orthopsidae a family of Mesozoic euechinoids in the order Orthopsida, characterized by a camarodont lantern and small, regularly spaced tubercles. North and South America, Europe, Africa, and India; Jurassic and Cretaceous.

Orthoptera an order of neopteran flying insects that includes the crickets and katydids in the suborder Ensifera, and the grasshoppers in the suborder Caelifera. Adapted for saltation, orthopterans are chewing insects with two pairs of wings; most genera have stridulatory organs on their wings, used to produce sound when rubbed with the hind legs. The earliest known are the Ensifera from the Late Carboniferous. Global distribution, Late Carboniferous to Recent.

Orthotetida an order of strophomenate brachiopods generally considered to include two suborders, Orthotetidina and Triplesiidina; global distribution, Ordovician to Silurian.

Oryctodromeus a genus of hypsilophodont ornithischian dinosaurs in the family Thescelosauridae, one of the earlier thescelosaurids. *Oryctodromeus* was relatively small, herbivorous, and basically bipedal but with forelimbs that seem to be adapted to digging. It is the only confirmed burrowing dinosaur. One site contains the remains of an adult and two juveniles in a burrow almost 7 feet long. United States, Late Cretaceous, Cenomanian, 99–97 Ma.

Osmunda an extant genus of large ferns in the order Osmundales. Notable for its erect rhizomes and naked sporangia, it evolved in Gondwana in the Triassic or possibly late Permian and spread worldwide. *Osmunda claytoniana* is an example of evolutionary stasis, having remained almost unchanged 180 million years after its appearance in the Triassic.

Ossicle a small bony structure; see **dermal ossicles**.

Ossicone a hornlike protuberance consisting of a bony core permanently covered with skin. Ossicones are found on modern giraffes and okapis and their ancestors, such as *Sivatherium*, and also on other mammals, such as *Uintatherium*.

Ossinodus a genus of stem-tetrapods tentatively placed in the family Whatcheeriidae. Known only from partial remains, it is the first stem-tetrapod to be found from Gondwana. Australia, Early Carboniferous, about 338 Ma.

Osteichthyes the bony fishes, the largest and latest major group of fish, appearing in the late Silurian. The osteichthyans are generally considered a superclass divided into two main groups, the ray-fins (actinopterygians) and lobe-fins (sarcopterygians). The earliest-known articulated osteichthyan is the Early Devonian *Guiyu oneiros*, but see also ***Andreolepis*** and ***Psarolepis***. The osteichthyans developed slowly in the Devonian during the dominance of the acanthodians and placoderms. But by the Carboniferous, the osteichthyan and chondrichthyan fish had supplanted the earlier groups, and they now account for more than half of all vertebrate animals.

Osteno fauna an assemblage of varied fossils found near Osteno, Italy. Some cephalopods are exceptionally well-preserved, notably ammonoids and coleoids; other specimens seem to be coprolites, thought to be from ichthyosaurs. Italy, Early Jurassic, 200 Ma.

Osteoderm a thin bony plate that forms part of the protective skin covering of many animals, extant and extinct. It is found mainly in reptilians, amphibians, and dinosaurs but is known also in some xenarthran mammals.

Osteoglossidae a small extant family of basal teleost fish in the superorder Osteoglossomorpha. It is the only family of freshwater fish found on both sides of Wallace's Line. It includes some of the largest extant freshwater fish, such as the arowanas, and is closely related to the Arapaimidae. The family includes several species, dated as early as 140 Ma. See also ***Phareodus*** and ***Joffrichthys***. Global distribution, Early Cretaceous to Recent.

Osteoglossomorpha an extant superorder of actinopterygian bony fish, among the most primitive teleosts. The group includes some of the largest of all living (*Arapaima*) and extinct (*Xiphactinus*) fish. One of the earliest-known genera is *Lycoptera*, especially important in Mesozoic biostratigraphy in China. The osteoglossomorphs are named "bony tongue" because many of them employ a specialized biting technique that involves the tongue and the roof of the mouth. Global distribution but since the Oligocene primarily in the Southern Hemisphere, Late Triassic to Recent.

Osteolepis "bony scale," a genus of primitive sarcopterygian fish in the subclass Rhipidistia and family Osteolepidae, related to the stem-tetrapods that began to colonize the land in the Devonian. About 8 inches long, *Osteolepis* is characterized especially by large square scales covered with cosmine, with small nerve canals running through the dermal covering. See also **Eusthenopteron** and **Tetrapoda**. Europe, Asia, and Antarctica; Late Devonian.

Osteolith a completely mineralized fossil bone.

Osteostraci a class of small- to medium-sized agnathans. They were fish-like marine vertebrates, distinguished by a large, bony headshield and a rounded mouth on the underside of the head. The osteostracans were among the most advanced agnathans. Global distribution, middle Silurian to Late Devonian.

Ostlingoceras a genus of heteromorph ammonitid ammonoids in the family Turrilitidae. Its auger-like shell is tightly coiled and helical. Cosmopolitan, Late Cretaceous, 100–94 Ma.

Ostracoda a large and very conservative subclass of small crustacean arthropods, many species of which have remained relatively unchanged since the Silurian. Both freshwater and marine, ostracods are the most common arthropods in the fossil record. They have two valves and superficially resemble bivalve mollusks until microscopic analysis reveals their crustacean features. Their body is unsegmented, with a large head and smaller thorax, and they use two pairs of well-developed antennae to swim. Their size varies from 0.1 to 32 mm, but the great majority are about 1 mm long, usually oval or rectangular. The largest genus is *Gigantocypris*, more than an inch long; with a fragile globular body, it has no fossil record. Ostracoda has two subclasses, **Myodocopa** and **Podocopa**, *q.v*. Global distribution, Ordovician to Recent.

Ostracoderms "shell skin," an informal term for several groups of armored jawless fish of the early Paleozoic, usually with a bony headshield. They were gradually replaced by placoderms and other jawed fish in the Devonian. Global distribution, late Cambrian (but first recorded in Early Ordovician) to Devonian.

Ostrea the oysters, a large extant genus of sessile bivalves in the order Ostreida; global distribution, Permian to Recent.

Otarioidea a superfamily of pinnipeds that is generally taken to include the extant Otariidae (fur seals and sea lions), the Odobenidae (walruses), and possibly other small groups. Extinct members are *Enaliarctos* and the Desmatophocidae. See also **Phocidae**. Cosmopolitan, middle Miocene to Recent.

Otavipithecus an obscure genus of Miocene apes, the earliest hominoid found in subequatorial Africa; Namibia, 13 Ma.

Othnielosaurus a genus of small ornithischian dinosaurs in the clade Neornithischia; synonyms *Laosaurus* and *Nanosaurus*. From 6 to 7 feet long but weighing less than 30 pounds, it was bipedal, with very small forelimbs. It is very similar to the poorly known *Drinker nisti*. Morrison Formation, United States, Late Jurassic, 156–151 Ma.

Otodus an early genus of large sharks in the extant order Lamniformes and family Otodontidae. Known from teeth and vertebrae, it is estimated to have been about 30 feet long and a macro-predator. See also ***Megalolamna. G***lobal distribution, Paleocene to Eocene or Miocene.

Ottoia a genus of predatory burrowing worms in the family Ottoiidae, considered a stem group priapulid. From 2 to 4 inches long, it used its muscular toothed proboscis to prey on hyoliths and trilobites. Known definitively only from the Burgess Shale; Canada, middle Cambrian, 508 Ma.

Ovalocephalus a genus of phacopid trilobites in the family

Pliomeridae. The body is oval, with a strongly pentagonal glabella, small eyes, 12–20 deeply furrowed thoracic segments, and a small pygidium. Italy, Spain, and China; Early Ordovician, about 475 Ma.

Oviraptor a genus of theropod dinosaurs, one of the earliest of the family Oviraptoridae. Edentulous and with a large beak and domed skull, it resembled an ostrich but had a shorter neck and a long tail. The name is misleading. A spectacular find in the Gobi Desert of an oviraptor fossilized above a nest of 15 to 22 oviraptor eggs was at first interpreted as preying on the eggs. It is now generally thought to provide direct evidence that oviraptors brooded their eggs and exhibited other bird-like behaviors. The nest has been disturbed by vertisol movement, and the interpretation is disputed. China, Late Cretaceous, 76–72 Ma.

Oviraptoridae a large family of maniraptoran theropod dinosaurs. They were edentulous but predatory, generally slender and ostrichlike with a parrotlike beak and a domed skull with a crest. The oviraptorids were closely related to the Caenagnathidae but more robust. Asia, known from widespread areas of China and Mongolia; Late Cretaceous, from around 90 Ma to the end of the period.

Oxyaenidae a family of relatively small carnivorous mammals formerly placed in the polyphyletic order Creodonta. They were catlike and plantigrade and had a broad head and large jaws, with teeth designed for crushing. North America, Europe, and Asia; Paleocene to Eocene.

Oxynoticeras a genus of ammonoids in the order Ammonitida, distinguished by a smooth, laterally compressed shell with a sharp keel. *Oxynoticeras oxynotum* is an index fossil in the Early Jurassic. Canada, Europe, and Africa; Early to Middle Jurassic.

Ozarkodina a genus of conodonts in the order Ozarkodinida that contains important index fossils for the late Silurian, including *O. crispa*, *O. bohemica*, and *O. snajdri*. The extinction of the genus is one of the indices marking the GSSP at the end of the Frasnian Age of the Late Devonian; see also ***Ancyrodella rotundiloba***. Global distribution.

Ozarkodinida an order of conodonts in the unranked clade Prioniodontida; global distribution, Ordovician to Middle Jurassic.

Ozawainellidae a family of foraminiferans in the order Fusulinida and superfamily Fusulinoidea; holarctic distribution, Carboniferous to late Permian.

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Pachycephalosauridae a family of relatively small ornithischian dinosaurs, named for a very thick skull roof. Bipedal and generally herbivorous, they have a great deal of skull ornamentation. They include the genera *Stegoceras*, *Pachycephalosaurus*, *Prenocephale*, and possibly *Dracorex*. Asia and North America, Late Cretaceous.

Pachycrocuta brevirostris the giant hyena of the late Pleistocene, the largest known at 240 pounds. It preyed on the giant elk and woolly rhinoceros, and the *Homo erectus* bones of the Longgushan Cave site in China (600,000 to 300,000 years ago) bear the tooth marks of a predator, possibly the giant hyena. China, Pliocene to middle Pleistocene.

Pachydyptes a monospecific genus of very large penguins (family Spheniscidae). *Pachydyptes ponderosus* was a flightless bird with large flippers adapted to swimming, about 5 feet long. New Zealand, late Eocene.

Pachypleurosauria a suborder of sauropterygian reptiles in the order Nothosauroidea, among the earliest aquatic reptiles. They were generally less than 3 feet long, slender, and lightly built, but *Keichousaurus* and some other genera grew up to 9 feet long. China and Italy, Middle to Late Triassic, 247–236 Ma.

Pachyophiidae see **Simoliophiidae.**

Pachyrhinosaurus "thick nose," a genus of ceratopsid dinosaurs in the subfamily Centrosaurinae. From 20 to 26 feet long and weighing up to 4 tons, it is notable for thick and ornamented bosses on the head and nose, and it also had several horns on a large neck frill. Several specimens have been found in northern Alaska and date from a time when climatic conditions were somewhat warmer than at present but still colder in winter than previously thought possible for dinosaurs. Alaska and Alberta, Late Cretaceous, 74–69 Ma.

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Paddlefish see ***Polyodon***.

Paenungulata a clade of afrotherian mammals that includes the Embrithopoda and possibly the Desmostylia, as well as the extant Proboscidea, Sirenia, and Hyracoidea. Global distribution, late Paleocene to Recent.

Pagetia a genus of very small agnostid trilobites in the family Eodiscidae. Less than half an inch long, it had eyes, only two thoracic segments, and an annulated pygidium with very prominent rings. *Pagetia* is well-known from the Burgess Shale but found worldwide, middle to late Cambrian.

Painted Hills an area in the John Day Basin of Central Oregon that preserves a great variety of fossils of the Eocene and Oligocene in multicolored layers of volcanic ash that accumulated in the large lakes of the area. The weathering of the volcanic deposits produced paleosols of different types and colors.

Pakasuchus an unusual monospecific genus of small crocodylomorphs with mammal-like dentition and other characteristics different from most crocodiles. Considered a notosuchian, *P. kapilimai* was the size of an elongated house cat. Tanzania, Early Cretaceous, 105 Ma.

Pakicetidae a family of cetartiodactyl mammals considered archaeocete whales. Found in freshwater deposits indicating a terrestrial habitat and lifestyle, they were semiaquatic but weak swimmers. The pakicetids were 2–6 feet long, with an elongated snout and long tail. The family includes three genera: *Pakicetus*, *Ichthyolestes*, and *Nalacetus*. Known only from Pakistan, early to middle Eocene.

Pakicetus a genus of cetartiodactyl mammals in the family Pakicetidae. It was quadrupedal, 3–6 feet long, and semiaquatic. The best known of the pakicetids *Pakicetus* is known from several partial skeletons and skulls with whalelike ear bones. Pakistan, early Eocene, 52–48 Ma.

Palaeacanthaspidae the most widespread family of primitive placoderms in the order Acanthothoraci, heavily armored with plates and thick spines. North America, Europe, and Asia; Early Devonian.

Palaechinoidea an early superfamily of regular echinoids in the subclass Perischoechinoidea. They had thick polygonal, tesselate plates beveling over each other to form a rigid test. Rare but widespread in North America and Europe, Silurian to early Permian.

Palaeeudyptes a genus of large early penguins (family Spheniscidae). Between 4 and 5 feet long, it was slightly larger than the modern emperor penguin. New Zealand, South America, Antarctica, and Australia; middle or late Eocene to late Oligocene.

Palaeobatrachus a genus of anurans in the extinct family Palaeobatrachidae. From 3 to 4 inches long, it was an early and long-lived genus of frogs. Europe, Early Cretaceous to Miocene or possibly Pleistocene.

Palaeobuthus distinctus a species of chelicerates in the order Scorpiones. Known only from the Mazon Creek assemblage, the scorpion *P. distinctus* is distinguished especially by its very long sting. United States, Late Carboniferous, 306 Ma.

Palaeocastor an early land beaver that excavated vertical helical burrows up to 10 feet deep. See also **Agate Fossil Beds**. North America and Asia, Oligocene.

Palaeocharaceae a group of charophytic algae descended from the Middle Devonian genus *Eochara*. Thought to be the ancestors of modern algae, they are marked by sinistrally spiraled gyrogonites. Global distribution, Early Cretaceous.

Palaeocharinus an early genus of trigonotarbid arachnids. Only a tenth of an inch long but equipped with fangs, it probably preyed on insects. Scotland, Early Devonian, 408 Ma.

Palaeochersis talampayensis a species of stem-turtles in the family Australochelyidae. One of the earliest-known turtles, it is an almost complete skeleton and skull, with one pes. It had a carapace about 2.5 feet long and shares several features with the coeval *Proganochelys*, its skull and skeleton containing both primitive and derived features. La Rioja, Argentina, Late Triassic, 215–206 Ma.

Palaeocircus an early hawk, a genus of predatory birds in the extant family Accipitridae; France, late Eocene to Oligocene.

Palaeocoma a genus of brittle stars in the order Ophiurida. With arms 4–5 inches long, *Palaeocoma* was a fairly large animal, with a well-defined, sub-pentagonal central disc up to half an inch wide. Europe, Middle Triassic to Early Jurassic.

Palaeocopida a large and disputatious order of straight-hinged ostracods, including the suborders Beyrichicopina, Kirkbyicopina, and many others (possibly the Kloedenellocopina, which are sometimes considered platycopid). Characterized mainly by a long, straight dorsal hinge, the shells of the Palaeocopida are often smooth but also sometimes have lobes, sulci, and ventral structures. Global distribution in the Paleozoic from the Early Ordovician, traditionally considered extinct at the end of the Permian.

Palaeoctopodidae a small family of basal octopuses in the order Octopoda. Known definitively only from Lebanon, Late Cretaceous.

Palaeodictyon a genus of ichnofossils generally found as a mesh of oval or circular traces; see also **Aberystwyth**. Cosmopolitan, Silurian to Recent.

Palaeodictyoptera a possibly paraphyletic order of medium-sized to large insects, the largest of five orders in the superorder Palaeodictyopteroidea. They are characterized by two pairs of dragonfly-like wings, sucking mouth parts, and a pair of winglets (paranotal lobes) on the prothorax. Several species had wingspans of more than 20 inches; among the largest known are *Moravia grandis*, *Lithomantis carbonarius*, and *Mazothairos.* See also ***Dunbaria***. Cosmopolitan, Late Carboniferous to late Permian.

Palaeodictyopteroidea a superorder of beaked insects in the subclass Pterygota, formerly Palaeodictyopterida. The first herbivorous insects and indeed the first terrestrial herbivores, they comprised 50% of the known Paleozoic species of insects. Some species were second in size only to the largest Meganisoptera. Their extinction at the end of the Permian left many niches to be filled by the insects of the Triassic. Global distribution, Middle Carboniferous to end Permian.

Palaeodonta a discarded term for a polyphyletic grouping of primitive artiodactyl mammals such as the oreodonts, all of which are now classified in either the suborder Tylopoda or the suborder Suina.

Palaeognathae the smaller of the two infraclasses of the Neornithes, the living birds. They first appeared around 70 Ma and spread worldwide, but they survive only in some flightless ratites and the tinamous. The extinct orders of the Palaeognathae are the Aepyornithiformes, Dinornithiformes, and Lithornithiformes. Almost all extant flying birds are classified as Neognathae.

Palaeoisopus a genus of pycnogonid arthropods, possibly related to the modern pycnogonid sea spiders. It was about a foot across with its legs spread. Known only from the Hunsrück Slate; Germany, Early Devonian.

Palaeomastodontidae a family of elephantoid proboscideans currently assigned to the Afrotheria. Probably ancestral to modern elephants, they had tusks and weighed more than 2 tons. Kenya, late Eocene to early Oligocene.

Palaeomerycidae a family of artiodactyl ungulates in the extant infraorder Pecora and superfamily Cervoidea. They are considered close to the line of descent to modern deer and giraffes. Global distribution except Australia, Eocene to Miocene.

Palaeonisciformes a paraphyletic order of primitive actinopterygian fish in the subclass Chondrostei. They are important especially because they have features that became common in most later actinopterygians. They are also basic to understanding the structure of the sarcopterygians and their descendants the terrestrial vertebrates. Global distribution, late Silurian to Late Cretaceous.

Palaeoniscum a genus of freshwater actinopterygian fish in the family Palaeoniscidae; synonyms *Palaeoniscus*, *Palaeothrissum*, and *Geomichthys*. About

a foot long, it had a blunt snout and heterocercal tail fin and is notable for its replaceable teeth. Europe and Asia, late Permian.

Palaeopantopoda an order of sea spiders, marine arthropods in the class Pycnogonida. They are not arachnids but are closer to them than to other arthropods. Europe, Devonian to Jurassic.

Palaeophonus one of the earliest arachnids, a genus of primitive scorpions in the superfamily Palaeophonoidea. Between 2 and 4 inches long, it had gills and is thought to have lived in water and on land, preying on small animals and fish. North America and Europe, middle Silurian to Middle Pennsylvanian.

Palaeoptera a term traditionally applied to all groups of flying insects that cannot fold their wings back over their abdomen. The classification of the palaeopterans is unsettled, but the group is probably paraphyletic. Most palaeopterans are extinct, the only surviving orders being the Odonata and the Ephemeroptera.

Palaeophragmodictyon a mound-shaped Ediacaran fossil with a mesh of spicules that is thought to be a primitive sponge. Australia, Ediacaran.

Palaeopython a genus of Eocene snakes in the suborder Serpentes and extant family Boidae. As long as 7 feet, it is especially notable for *P. fischeri*, a three-trophic-level fossil found at the Messel Shale Pit: inside the snake's stomach is a lizard (*Geiseltaliellus maarius*), inside which is an unidentified insect. Europe, 48 Ma.

Palaeoryctidae a family of nonplacental eutherian mammals tentatively placed in the order Cimolesta. Part of the placental evolutionary radiation late in the Cretaceous, they were shrewlike and mainly insectivorous, but their dentition resembles that of later carnivores. North America, Asia, and Africa; Late Cretaceous to Paleocene.

Palaeosaniwa a monospecific genus of carnivorous lizards in the family Varanidae. About 10 feet long, *P. canadensis* resembled modern monitors, and its dentition is essentially like that of a Komodo dragon. Western North America, Late Cretaceous, 75–70 Ma.

Palaeoscolex a genus of middle Cambrian worms in the class Palaeoscoleoida; the class is also called Palaeoscolecida.

It is known from many segmented fragments and possibly a whole specimen in the Chengjiang biota. China and Russia, middle Cambrian to Silurian.

Palaeosmilia a horn coral, a genus of solitary rugose corals traditionally placed in the order Stauriida and family Palaeosmiliidae but possibly a doubtful genus; type species *P. murchisoni*. Large and usually spiral or trochoid, it is characterized by

radially arranged septa, an irregularly ringed surface, and a deep pit. Europe, North Africa, Asia, and North America; Late Devonian to Permian.

Palaeospondylus an enigmatic genus of primitive fish-like vertebrates, tentatively placed in the class Pteraspidomorphi. It is known only from the area of Caithness, Scotland, where hundreds of specimens have been found. It was jawless, eellike, and 2–3 inches long, but whether its skeleton is calcified or cartilaginous is unclear. Middle Devonian.

Palaeotarbus jerami a species of arachnids in the order Trigonotarbida; originally named *Eotarbus*. The oldest-known arachnid, it was among the first terrestrial animals. England, late Silurian, 419–416 Ma.

Palaeothele montceauensis a species of mesothele spiders in the order Araneae. Originally named *Eothele*, it is the earliest-known mesothele, known from two specimens from Montceau-les-Mines. France, Late Carboniferous.

Palaeotheriidae a family of herbivorous perissodactyl hippomorphs, possibly in the line of descent to the Equidae. The type genus *Palaeotherium* resembled a small rhinoceros. Europe and Asia, Eocene through Oligocene.

Palaeothrissum see ***Palaeoniscum***.

Palaeotragus a genus of artiodactyl mammals in the family Giraffidae. About 10 feet high and almost 7 feet at the shoulder, it resembled a large okapi or small modern giraffe. Some species bore two ossicones and some had none. Asia, Europe, and Africa; Miocene to Pliocene, 14–5 Ma.

Paleaster *see* ***Hudsonaster.***

Paleobiochemistry the study of biochemical processes and their evolution in the fossil record, using the methods of organic chemistry to identify and study molecular fossils. Research in DNA, proteins, and other molecules is useful in many ways, including cladistic analysis, location of fossil fuels, coloration of fossils, and environmental changes. See also **S*olenopora*.**

Paleobioclimatology the study of the changes in climate in the geological past and of the effects of these changes on animal and plant life.

Paleobiocoenosis an assemblage of fossils of an interrelated community of organisms that lived together.

Paleobiogeography the study of the effects on organisms of the dynamic interaction of geologic processes such as plate tectonics with biological, climatic, and environmental conditions.

Paleobiology the branch of paleontology concerned with the biology of extinct organisms and their relationship to modern organisms.

Paleobotany the study of plant fossils and their interrelationships with other organisms in the geological past, also called paleophytology.

Paleocene the first epoch in the Cenozoic Era, from 66 to 56 Ma. The GSSP marking the beginning of the era is the worldwide occurrence of an iridium layer associated with a large asteroid impact. The end-Cretaceous extinction affected plant life less severely than animal life, so that in the Paleocene conifers and cycads continued to dominate in the higher latitudes. Angiosperms spread, especially in the Southern Hemisphere; the first grasses appeared toward the end of the period. The first modern sand dollars, clypeasteroid echinoids, appeared in the sea, and ants diversified rapidly on land. Large flightless birds appeared, and mammals diversified rapidly, filling the many ecological niches left vacant at the end of the Cretaceous. The average size of mammals increased. Most modern fish groups were present and continued with relatively little change through the Cenozoic.

Paleoclimatology the study of past climatic conditions throughout geologic time and of the causes of worldwide and local climatic variation. It involves especially sedimentology, palynology, glaciology, limnology, pedology, phytogeography, and the study of certain marine organisms such as coral.

Paleodepth the water depth at which a geologic stratum was deposited.

Paleoecology the study of the relationships between fossil organisms and their environment, especially concerned with faunal assemblage zones (e.g., the Dicynodon Zone).

Paleogene the first period of the Cenozoic Era, including the Paleocene, Eocene, and Oligocene Epochs.

Paleogeography the study of the changes in the distribution of the Earth's land masses caused by tectonic plate movement.

In the billions of years of Earth's existence, sections of the crust have moved constantly in the shifting of tectonic plates, sometimes called continental drift. Throughout Paleozoic time, the most constant large land mass was the southern section, called Gondwana; it was located generally in the lower part of the Southern Hemisphere and included what is now South America, Africa, Antarctica, Australasia, Madagascar, and India. The Northern Hemisphere long contained only smaller fragments of land – what is now North America, Greenland, Europe, and Northern Asia.

But around 400 Ma, in a great mountain-building event called the Variscan orogeny, the northern fragments began to coalesce into a land mass called Laurasia and

drift southward. By the end of the Carboniferous, around 300 Ma, all of the large land masses were close together, forming the most recent global supercontinent, Pangaea, which extended in the Permian from the South Pole almost to the North Pole. Then, during the Early Jurassic, the two sections began to drift apart, separating the organisms on the Laurasian segment from Gondwana. The three main sections of Laurasia – North America, Europe, and Asia – continued to drift apart from each other in the Cretaceous, isolating the dinosaurs and other land animals on each segment.

Since the beginning of the Cretaceous, although sporadic and fluctuating, the movement of the continents has generally been away from each other. Late in the Cretaceous, Africa and India broke off from Gondwana, with India moving northward; Antarctica separated from Australia at the end of the Eocene and from South America in the early Oligocene, isolating their animals and plants. All of the present continents existed in the Paleocene, but as they moved, some have changed in size, notably North America and Asia, which have grown by accretion; nevertheless, the total global land mass today is comparable to that of the Triassic.

Paleoichnology the study of trace fossils showing evidence of the actions of organisms in the geological past, such as fossilized footprints, tracks, and burrows. Paleoichnology is increasingly important in research on fossil ecosystems, providing evidence of the activities and interactions of organisms in the past. Since trace fossils are seldom connected with actual animals, they are given binomial names but not assigned to higher taxonomic categories. See also **ichnoentomology**.

Paleomorphology the study of the structure and form of extinct plants and animals.

Paleontology the study of ancient life in the form of fossils, especially the evolution of new species and their distribution in space and time.

Paleopalynology the stratigraphic study of fossilized pollen, single-celled algae, spores, particulate organic matter, and other wind-borne palynomorphs. It is especially important in the study of plant evolution and the correlation of geological strata and is also significant in studying climate change.

Paleoparadoxia a genus of large to medium-sized herbivorous mammals in the order Desmostylia. A large marine relative of elephants that appeared in the Miocene and became extinct about 11,000 years ago, *Paleoparadoxia* had very large forelimbs, and its eyes were near the top of the head. Notable for the backward angle of the teeth, it probably ate seaweed and sea grasses. It is now thought to have been almost fully marine like the modern sirenians. Northern Pacific coastal regions from Japan to Alaska and as far south as Baja California.

Paleopedology the study of paleosols, fossil soils of the geological past, either as part of a sequence of sedimentary strata or as a persistent soil surface that is no longer actively forming.

Paleophytic term sometimes used for a paleobotanic division of time in the early Paleozoic Era, a time of transition from algae to gymnosperms. Pteridophytes were especially abundant in the Paleophytic from the late Cambrian up to the time of the appearance of gymnosperms in the Late Devonian.

Paleopneustina a suborder of atelostomate sea urchins in the order Spatangoida. Possibly paraphyletic, it includes principally the families Schizasteridae and Paleopneustidae. Cosmopolitan, Late Cretaceous to Recent.

Paleosol a fossil soil horizon in the geologic past, typically altered in place by biological, chemical, and physical processes. Paleosols vary according not only to their geological structure and chemical composition but also to the community of plants and animals that occupied them.

Paleothyris one of the earliest amniotes, a genus of primitive anapsid reptiles in the family Protorothyrididae, known only from Nova Scotia. Similar to *Hylonomus*, a slightly earlier reptile found also in Nova Scotia, *Paleothyris* was about a foot long and probably ate insects and other small animals. Canada, middle Pennsylvanian, 312 to 304 Ma.

Paleozoic Era see **Geologic Time Scale**.

Paliguana whitei a species of lizard-like eosuchians in the clade Eolacertilia. Considered a basal lepidosauromorph, it is known only from a 1-inch skull first described by Robert Broom in 1903. South Africa, Early Triassic, 251 Ma.

Palmate of a leaf divided into separate lobes or leaflets spreading from the base like fingers of a hand.

Palmatolepis an abundant genus of conodonts in the Late Devonian. Most of its species became extinct in the Hangenberg Event at the end of the period.

Palynofacies an assemblage of palynomorphs and other organic matter in a sedimentary stratum.

Palynomorphs organic microfossils from 5 to 500 microns in size, consisting of pollen, spores, sporopollenin, silica, chitin, or pseudochitin.

Palynostratigraphy the application of palynologic techniques to the study of geological strata. Wind-borne palynomorphs, spread over great distances, are especially useful in correlating marine and nonmarine sediments.

Pampaphoneus biccai "plains killer," a species of dog-sized carnivorous dinocephalians in the family Anteosauridae. *Pampaphoneus* is known from one specimen, a skull identified in 2012 in Brazil. Middle Permian.

Pampatheriidae ancestral armadillos, a family of large armored xenarthran mammals in the extant order Cingulata. Originating in South America in the Eocene, some weighed more than 400 pounds. Probably the largest was *Holmesina*, which was almost 7 feet long and weighed almost 500 pounds. When the Panama land bridge formed in the Pliocene, some genera emigrated to North America. All the larger pampatheres, along with their relatives the glyptodonts, became extinct in the Quaternary extinctions. Eocene to Pleistocene.

Pandanaceae an extant group of tropical plants in the order Pandanales. Although called screw pines, they are mostly palm-like and of medium height, and some genera are lianescent. Tropical areas from Oceania and Australia across the Indian Ocean to West Africa, Cretaceous to Recent.

Panderichthys a genus of Devonian fish close to the line of descent to all tetrapods. *Panderichthys* was characterized by two pairs of lobed fins and an unusual pattern of skull bones, which enabled it to facultatively breathe air by means of an external nasal slit. Between 3 and 4 feet long and similar to the larger *Tiktaalik*, *Panderichthys* represents a transitional stage of evolution from *Eusthenopteron* to tetrapods. Latvia and North America, Late Devonian, 384–383 Ma.

Panderodus an early genus of conodonts in the family Panderodontidae. Its elements are generally simple and horn-shaped, with fine striations, some of which are caused by radial lamellae. Ordovician to Silurian.

Pangaea a term for the supercontinent created by the convergence of almost all land masses between the Late Carboniferous and Early Jurassic. See **paleogeography.**

Pannotia "all southern," the most common name for a short-lived (roughly 650 to 560 Ma) Neoproterozoic supercontinent completely within the Southern Hemisphere, with the African craton centered on the South Pole.

Panphagia a monospecific genus of early sauropodomorph dinosaurs in the family Guaibasauridae, generally considered a prosauropod. Found in a middle Carnian layer of the Ischigualasto Formation, *P. protos* is one of the earliest dinosaurs. Named "eating all" because its dentition and body structure suggest an omnivorous diet, it may represent a transitional stage between the carnivorous theropods and the herbivorous sauropods. Argentina, Late Triassic, 231 Ma.

Panthalassa the Panthalassic Ocean, surrounding the supercontinent Pangaea from the Permian to the Jurassic Period.

Panthera leo atrox a species of large, lion-like carnivores in the family Felidae, also called Naegele's giant jaguar. Related to the Eurasian cave lion, it was short-legged and heavy-bodied. Up to 25% larger than the modern African lion, it grew to 4 feet at the shoulder and 9 feet long head to tail. North America, late Pleistocene to 11,000 years ago.

Pantodonta an order or suborder of mostly herbivorous eutherian mammals, generally considered cimolestids. Early forms weighed about 20 pounds, and some later species, such as *Coryphodon*, weighed more than 1000 pounds. Global distribution except Australia, Paleocene to Eocene.

Pantolestidae a family of semiaquatic, nonplacental eutherian mammals in the order Cimolesta. Piscivorous, some grew to 3 feet long, the later species coming to resemble the modern otter. North America and Europe, Late Cretaceous to Oligocene.

Pantotheres a polyphyletic group of mouse- and rat-sized mammals. Some of them, such as the Dryolestidae and Amphitheriida, may be close to the line of descent of primitive marsupial and placental mammals.

Pan troglodytes the larger of the modern chimpanzees, which split off from their Bonobo cousins about 1 Ma. The chimpanzees had branched off the human line of descent between 7 and 6 Ma.

Papio angusticeps the earliest-known baboon, identified from a skull fragment found in the cave at Malapa where *Australopithecus sediba* was found. This fossil, 2.0–2.3 million years old, differs very little from the modern baboon. The fossil record of baboons is sparse, but they seem to have appeared very recently. South Africa, Pleistocene.

Pappochelys rosinae a species of small diapsid reptiles that seems to be intermediate between earlier diapsids like *Eunotosaurus* and stem-turtles like *Odontochelys*. Its body was 6 inches long and its tail another 6 inches. *Pappochelys* is characterized by two pairs of temporal fenestrae and by flattened ribs and gastralia that are beginning to fuse together, a step in the process that led to the carapace and plastron of later turtles. It is known from two dozen specimens found at an outcrop in southern Germany of the Lower Keuper stratum. A 2019 report on one partial specimen describes an advanced cancerous growth on a leg bone. Germany, Middle Triassic, 240 Ma.

Pappotherium a monospecific genus of small early eutherian mammals, possibly in the metatherian order Deltatheroida. It is known only from a jawbone and two teeth found in Texas. United States, Early Cretaceous, 113–109 Ma.

Paraceratherium a genus of very large hyracodont perissodactyl mammals in the subfamily Indricotheriinae; synonyms *Indricotherium* and *Baluchitherium*. Resembling a large, hornless rhinoceros, it was one of the largest land mammals ever: 18 feet high at the shoulder, 26 feet long, and weighing 25–30 tons. Herbivorous, it probably had a prehensile upper lip and seems to have been hairless. Asia, early Oligocene to early Miocene, 30–22 Ma.

Paracrinoidea "near crinoid," a small class of blastozoan echinoderms. They superficially resembled stalked crinoids in having a stem, thecae, and arms. North America and Europe, Early Ordovician to early Silurian.

Paradoxides a genus of large early trilobites in the order Redlichiida, the largest species up to 15 inches long. *Paradoxides* is characterized by a very long thorax and two spines longer than its body, extending backward from the cephalon; its large glabella expands forward. It is prominent in the Avalonian beds of the middle Cambrian. North and South America, Europe, and North Africa; middle to late Cambrian.

Parahagla see ***Habrohagla***.

Parakidograptus acuminatus a species of pterobranch graptolites in the order Graptoloidea. Its first appearance marks the beginning of the Silurian at 443.8 Ma. Scotland.

Paralititan strömeri a species of titanosaurian dinosaurs, an extremely massive sauropod found in 1999 at the Bahariya Oasis in Egypt, near where Ernst Strömer had made important finds in the early twentieth century. A 6 foot humerus and other upper body bones make it clear that it was one of the largest dinosaurs. Estimated at 85 feet long and 65 tons, it may be almost as large in mass as another titanosaurian, *Argentinosaurus*. Egypt, Late Cretaceous, 94 Ma, soon after the separation of Africa and South America.

Parallelodon a genus of marine bivalves in the order Arcoida and family Parallelodontidae. It is suboval to rectangular and up to 1.2 inches long, with a long, straight hinge line and fine concentric growth lines. Global distribution, Early Ordovician to Late Cretaceous.

Paramyidae a sciuromorph family of the earliest-known rodents, tentatively placed in the infraorder Protrogomorpha and perhaps the basal stock of the order Rodentia. Scansorial and squirrel-sized, they may have lived in trees and competed with early primates. North America, Europe, and Asia; late Paleocene to late Eocene.

Paramylodon a genus of giant ground sloths in the order Pilosa and the extinct family Mylodontidae; formerly called *Mylodon*. About 10 feet long and weighing more than a ton, it is also notable for the dermal ossicles embedded in its thick skin.

It is known from widespread North American deposits from Canada to Central America; late Pliocene to late Pleistocene.

Paranthropus a genus of hominins similar to and possibly descended from gracile australopithecines. *Paranthropus* is known from several skull and other fragments dated between 2.3 and 1.2 Ma. East Africa.

Paranyctoides a genus of Late Cretaceous eutherian mammals. The earliest-known erinaceomorph, the scansorial *Paranyctoides* had some characteristics of true insectivores. North America and Uzbekistan, 89–66 Ma.

Paranyroca a genus of anseriform birds in the extant family Anatidae or the new family Paranyrocidae. It is known only from two specimens found in South Dakota. United States, middle Miocene.

Paraparchitoidea a superfamily of robust ostracods in the order Kloedenellocopina; global distribution, Devonian to late Permian.

Paraphyletic group see **polyphyletic group.**

Parapithecidae a family of primitive anthropoid primates in the superfamily Parapithecoidea, known especially from the middle Oligocene Fayum deposits of Egypt. The parapithecines are difficult to classify but may be the most primitive advanced primates known. Africa and Asia, Eocene to Oligocene.

Parapuzosia a genus of very large ammonoids in the order Ammonitida and family Desmoceratidae. It is the largest-known ammonoid, with fossil shells almost 7 feet in diameter. Global distribution, Late Carboniferous.

Parasaurolophus a genus of duckbilled herbivorous dinosaurs in the family Hadrosauridae and subfamily Lambeosaurinae, notable for the long, distinctive crest from the nose to behind its head. Several theories try to explain the function of this enigmatic crest, such as to generate trombone-like sounds, to support a decorative flap of skin, or to provide a sign of sex recognition. It is known from a few specimens of three species; the type species, *P. walkeri*, was about 31 feet long and weighed almost 3 tons. North America, 76 Ma.

Paraschwagerina a genus of fusulinid foraminiferans, index fossils in the early Permian. They occupied a deep marine environment, far offshore. North America, Europe, and Asia; early to middle Permian.

Paraselkirkia a genus of predatory priapulid worms in the family Selkirkiidae. Similar to but larger (6 inches) than the Burgess Shale ***Selkirkia***, it is known only from the Chengjiang biota. China, early Cambrian, ca. 518 Ma.

Parasemionotidae a family of small, bony neopterygian fish in the order Semionotiformes; cosmopolitan, Early to Middle Triassic.

Parasuchia see **Phytosauria**.

Paratheres see **Xenarthra**.

Parathuramminoidea an important superfamily of foraminiferans in the order Fusulinida. They generally had a test with a globular or tubular chamber, sometimes in a series of chambers. Global distribution, Ordovician to Permian.

Paratype a specimen of a type species other than the holotype. Several paratypes may be used in identifying the species.

Paraxiphodon see **Xiphodontidae**.

Parazoa a subkingdom of eukaryotic multicellular animals whose only known living members are the sponges and the placozoan *Trichoplax*. Parazoans early evolved into a line separate from all other animals, splitting off from the Eumetazoa in the early Neoproterozoic, about 940 Ma. Although they have differentiated cells, they have no organs or tissues.

Pareiasauridae a family of bulky, armored herbivorous reptiles in the suborder Procolophonia, formerly included in the paraphyletic order Captorhinida. As long as 10 feet and as heavy as 1300 pounds, some species are notable for a great number of scutes covering the body and for heavy cephalic ridges and knobs. Some later pareiasaurs developed erect posture, with their legs directly under the body; see ***Bunostegos*** and ***Scutosaurus***. Africa, Europe, and Asia; middle to late Permian.

Paris Canyon a site in Idaho being developed in 2018, dated at only 1.3 million years after the end-Permian extinction. The great diversity of its fossil assemblage may indicate a more rapid recovery of marine life after the extinction than previously thought. United States, Early Triassic.

Parkinsonia a genus of ammonoids in the order Ammonitida and family Parkinsoniidae; synonym *Gonolkites*. The first occurrence of *Parkinsonia* marks the beginning of the Bathonian at 167.7 Ma. The shell is evolute, laterally compressed, and strongly ribbed and has a diameter of 5–6 inches. United States (Alaska), Europe, and Asia; Middle Jurassic, 167.7–165 Ma.

Parksosaurus a genus of hypsilophodont ornithopod dinosaurs in the family Thescelosauridae, closely resembling *Thescelosaurus*, another ornithopod also from the Maastrichtian. Herbivorous and bipedal, it was about 8 feet long and slender. Alberta, Late Cretaceous, 70 Ma.

Parvancorina "small anchor," a genus of enigmatic Ediacaran organisms with some arthropod-like characters. Known from circular molds, less than an inch wide, and marked by a central ridge with a raised semicircular arc at one end of the ridge, it is similar in shape to trilobites but probably unrelated. It is found in marine sediments in Russia and Australia and also on the underside of some Australian paleosols. 560–555 Ma.

Patagium a skin membrane attached to the limbs of an animal, giving it some gliding ability. In many gliding mammals, it is attached to the forelimbs and the hindlimbs. With skeletal adaptations, especially in the wrist bones, it is known as a gliding mechanism in many mammals from the Jurassic to the present. See, for instance, ***Volaticotherium***, ***Maiopatagium***, and ***Miopetaurista***.

Patagonykus a monospecific genus of theropod dinosaurs in the family Alvarezsauridae. Known from a partial skeleton, *P. puertai* was about 7 feet long. Argentina, Late Cretaceous, 94–87 Ma.

Patagotitan mayorum a species of large titanosaurian sauropod dinosaurs described in 2017. Known from partial skeletons of several individuals and estimated at 120 feet long and 69 tons, it may be the largest-known dinosaur. Argentina, Early Cretaceous, 102 Ma.

Patellidae an extant family of limpets, gastropods in the superfamily Patelloidea; global distribution, Permian to Recent.

Patellina an extant genus of dish-shaped spirillinid foraminiferans in the family Patellinidae; global distribution, Late Jurassic to Recent.

Patellogastropoda an order of gastropod mollusks; formerly called Docoglossa. The order includes the true limpets of the Patelloidea, the more recent superfamily Lottioidea, and other smaller groups. Global distribution, Ordovician to Recent.

Patelloidea the limpets, an extant superfamily of gastropod mollusks in the order Patellogastropoda. These gastropods are specialized for clinging to rocks under a low, cap-shaped shell with radiating ridges. See also **Neritimorpha**. Global distribution, Permian to Recent.

Paterinata the earliest class of brachiopods, in the subphylum Linguliformea, found worldwide in the Cambrian. The Paterinata were inarticulate, impunctate, and generally astrophic; they had no delthyrium. They appeared in the Tommotian of the early Cambrian and dwindled in the Ordovician, becoming extinct at the end of the period.

Paterinida an order of early inarticulate brachiopods in the class Paterinata. They are characterized by biconvex, rounded, generally phosphatic shells. Global distribution, early Cambrian to Middle Ordovician.

Patriomanis a monospecific genus of pangolins in the suborder Eupholidota and family Patriomanidae. *Patriomanis americana*, well-known from several partial specimens found between 1970 and 2016, is the only known North American pangolin, although modern pangolins are widespread in Asia and Africa. Long claws and other arboreal traits suggest that it probably spent most of its time in trees. See also ***Eomanis***. United States, Late Eocene to Oligocene.

Paucituberculata an extant order of marsupials prominent in South America in the Oligocene and Miocene but declining rapidly thereafter; extant only in the family Caenolestidae, they are now restricted to parts of southern South America. Paleocene to Recent.

Peak zone a stratigraphic zone in which a specific organism occurs in its greatest abundance or which is dominated by an exceptional abundance of one or more types of organisms.

Pecopteris a common form genus of fossil foliage, especially from the marattialean fern *Psaronius* but also from some seed ferns (see ***Alethopteris***) and several filicalean ferns. Especially prominent in the Carboniferous and Permian; global distribution, Devonian to Miocene.

Pectinidae the scallops, an extant family of bivalves in the superfamily Pectinoidea. The Pectinidae are characterized by a single adductor muscle and a basically triangular shell, which is usually ridged and from 1 to 5 inches wide. They are benthic but facultatively mobile, most genera differing from other bivalves by swimming freely. Although the Pectinidae were the most diverse Mesozoic bivalves, they almost disappeared at the end of the Cretaceous; they then again radiated rapidly in the Cenozoic. Global distribution, Triassic to Recent.

Pederpes finneyi a species of stem-tetrapod amphibians in the family Whatcheeriidae. An important specimen for its occurrence in the period of time called Romer's gap. About 3 feet long and with a large, subtriangular head, this tetrapod has several features indicating greater terrestriality than any earlier animal, especially in the wrist and ankle joints. Scotland, Early Carboniferous, about 348 Ma.

Pedetidae an extant family of sub-Saharan rodents in the order Sciuromorpha. The modern springhares differ only slightly from the earliest Pedetidae, which arose in the Miocene. Southern Africa, early Miocene to Recent.

Pedicle the stalk that most brachiopods use to attach the pedicle valve to a hard substrate, usually below the animal.

Pedinoida an important order of Mesozoic echinoids, probably including ancestral euechinoids. Still extant, it appeared in the Early Triassic, diversified widely in the Jurassic, and declined in the Cenozoic. They are closely related to the Diadematoida and Echinothurioida. Cosmopolitan but mainly Europe, Early Triassic (222 Ma) to Recent.

Pedipalps a pair of anterior limb-like appendages in some chelicerates, especially the arachnids. In spiders they are generally leg-like feelers, and in other arachnids they are pincers, sometimes large and dangerous.

Peking Man see ***Homo erectus pekinensis*.**

Pelagic living in open water, typically in the water column of the ocean, neither nearshore nor at the bottom. Pelagic animals include birds as well as free-swimming or floating organisms. See also **benthic, nektic**, and **planktic**.

Pelagornis a widespread genus of large sea birds, ornithurans in the family Pelagornithidae. Appearing at the end of the Oligocene, it diversified rapidly. One of the Miocene species, *P. sandersi*, had probably the widest wingspan known in a bird, as much as 24 feet (see also ***Argentavis magnificens***). *Pelagornis* is notable for the bony spikes in its mouth which it used to grasp its prey, live or dead fish. Global distribution, late Oligocene to late Pliocene.

Pelecanimimus polyodon a species of ornithomimosaurian dinosaurs known from the articulated front half of a skeleton. Estimated at 8 feet long, *Pelecanimimus* is considered a basal ornithomimosaurian, having more than 200 heterodont teeth rather than a beak. It is characterized also by a small keratinous head crest, straight claws, and a small gular pouch that gives it its "pelican" name. The later ornithomimosaurians developed a beak and were toothless. See also ***Harpymimus***. Las Hoyas, Spain; Early Cretaceous, 130 Ma.

Pelecypod a term informally used to refer to mollusks in the class Bivalvia, formerly called Pelecypoda.

Pelmatozoan "stem animal," a term formerly referring to the paraphyletic subphylum of echinoderms called Pelmatozoa, which were attached to the sea substrate by a stem. The term is still used to refer generally to organisms with this habit. Global distribution, early Cambrian to Recent.

Peltephilus a genus of fossorial horned armadillos, South American xenarthran mammals in the extant order Cingulata and family Chlamyphoridae. *Peltephilus* was armed with large claws and bony scutes on its head and bands of scutes across

its back; it also bore at least one pair of small horns on the top of its snout, forward of the eyes. The function of the horns is unclear, although they offered at least some defense for the eyes. These horns represent an example of convergent evolution in two unrelated animals since the size and placement of the horns are like that of *Ceratogaulus*, the horned rodent of the Neogene of North America and the only other known fossorial horned mammal. Argentina, Chile, and Bolivia; Oligocene to middle Miocene.

Peltobatrachus "shielded frog," a genus of armored temnospondyl amphibians in the family Peltobatrachidae. About 2 feet long, it bore a series of narrow plates covering its entire body. East Africa, late Permian.

Peltoceras athleta a species of ammonoids in the superfamily Perisphinctoidea and family Aspidoceratidae. It was evolute, about 6 inches in diameter, and strongly ribbed and tubercular. Europe, North and South America, Madagascar, and Asia; Late Jurassic, 161–156 Ma.

Pelycosaurs an informal term for a paraphyletic stem group of synapsids that were the dominant terrestrial animals of the Carboniferous and Permian. Among the earliest amniotes, pelycosaurs arose in the Pennsylvanian and are considered ancestral to therapsids and eventually to mammals. Their bowl-shaped pelvic structure gave them greater agility and speed on land than earlier reptiles like *Hylonomus*. They are most noticeable for the high and partly vascularized sails stretched on elongated neural spines down the back of several genera; in species like *Dimetrodon* and *Edaphosaurus*, these formed a spectacular sail of several square feet. Another important feature of some pelycosaurs was one or two pairs of longer, grasping teeth at the front of the snout, precursors of the canine teeth that have been one of the hallmarks of the synapsid-mammal lineage ever since. North America and possibly Europe, Early Pennsylvanian to late Permian.

Pengana an early hawk, a genus of predatory birds in the extant family Accipitridae; known only from Australia, early Miocene.

Pennatulacea the sea pens, an order of soft-bodied, anthozoan cnidarians in the subclass Octocorallia, some of which are feather-shaped. They live in colonies of dimorphic polyps, most of them attached to the substrate by a stalk but some capable of movement. Global distribution, Cambrian to Recent.

Pennsylvanian see **Carboniferous.**

Pentaceratops a genus of large ceratopsian dinosaurs in the subfamily Chasmosaurinae. Well-known from several skulls and skeletons found in New Mexico, *Pentaceratops* grew up to 20 feet long and 5–6 tons. Two of its five horns were very long and its neck frill very large. United States and Canada, Late Cretaceous, 71–66 Ma.

Pentacrinites a genus of articulate stalked crinoids in the order Isocrinida and family Pentacrinitidae; formerly called *Pentacrinus*. It is notable for a small cup and five long, repeatedly branching arms at the end of a stem as long as 3 feet; the stem is pentagonal or star-shaped in cross-section. *Pentacrinites* is thought to have grown on driftwood and thus be semi-planktic. Global distribution, Middle Triassic to Eocene.

Pentamerida an order of biconvex articulate brachiopods in the class Rhynchonellata. The pentamerids are generally characterized by impunctate, subpentagonal shells, and a short hinge line. Global distribution, middle Cambrian to Late Devonian.

Pentastomida the "tongue worms," a small and controversial phylum of parasites on some terrestrial animals and fish. Pentastomes had internal plates separating the body cavity pentamerally when seen in cross-section. Many biologists have considered them to be an offshoot of the branchiurans, a group of crustaceans. Since 1994, however, discoveries of several pentastomes in upper Cambrian strata in Canada and the Orsten Lagerstätten of Sweden (see also ***Heymonsicambria*** and ***Linguatula***) have shown that the pentastomes have persisted almost unchanged until the present, convincing many authorities that they should be accorded phylum status. Global distribution, late Cambrian to Recent.

Pentecopterus decorahensis one of the earliest-known species of eurypterids, chelicerates in the suborder Eurypterina and family Megalograptidae. Discovered in the early twenty-first century near Decorah, Iowa, it was as long as 6 feet and had a dozen clawed arms and a 3 foot tail used in swimming. Unlike some larger Paleozoic eurypterids, it was an efficient predator. United States, Middle to Late Ordovician, 460 Ma.

Pentoxylales an order of gymnosperms that were small shrubs or trees. Their affinities are unclear, but they are related to ginkgos and may be in the line of descent to angiosperms. A stem genus *Pentoxylon* and a seed-bearing cone genus *Camoconites* have been described for the treelike genus *Taeniopteris*. The Pentoxylales were an important part of the Gondwana flora in the Jurassic. Known only from India and New Zealand, Jurassic and possibly Early Cretaceous.

Pentremites a genus of blastoid echinoderms in the order Spiraculata and family Pentremitidae. It was attached to the substrate by a slender stalk from 4 to 12 inches long. North America, Early Carboniferous.

Peppered moth see ***Biston betularia***.

Peradectes a genus of early marsupials in the family Peradectidae. The type species, *P. minor*, was only 8 inches long from head to tail. Thought to be a scansorial

omnivore, it appeared just after the end-Cretaceous extinction, between 65 and 63 Ma. North and South America and Europe, early Paleocene.

Peramelemorphia an extant order of small marsupial mammals that includes the modern bandicoots and bilbies. The order includes several extinct genera from the Oligocene and Miocene. Australia and New Guinea, Oligocene to Recent.

Periodic extinction the theory that major extinctions have occurred since the Permian at regular intervals of about 26 million years.

Peripatus an extant genus of velvet worms (phylum Onychophora) in the family Peripatidae. It was similar to *Aysheaia* of the middle Cambrian, but Paleozoic collection failure leaves the possible relationship unclear. Central and South America, Burma, Australia, and New Zealand; Late Cretaceous to Recent.

Periptychidae an early family of tapir-like protoungulate placental mammals. They are characterized by vertical, wrinkled ridges on their molars and ranged in size from 30 to 200 pounds. Some periptychids were omnivorous, and others were herbivorous. North America and possibly Eastern Asia, Late Cretaceous through Paleocene.

Perissodactyla an order of ungulate mammals having an odd number of toes, especially herbivorous terrestrial ungulates having a large central digit on each foot, such as the horse, tapir, and rhinoceros. The earliest perissodactyls appeared in the late Paleocene (see **Artiodactyla** and ***Hyracotherium***).

Perittodus apsconditus "hidden odd tooth," one of several new stem-tetrapods discovered by Jennifer Clack in 2016; its complex dentition is different from other tetrapods. See also **Tetrapoda**. England, Late Devonian.

Permarachne novokshonovi a species of proto-spiders in the order Uraraneida and family Permarachnidae. Known only from a Russian specimen (a molt half an inch long) described in 2005. See also ***Attercopus***. Ural Mountains, Permian, 280 Ma.

Permian the final period of the Paleozoic Era, from 299 to 252 Ma. Although it was a relatively hot and dry time, sea levels sank, evidently because of ocean floor changes accompanying the formation of the supercontinent Pangaea. Pelycosaurian synapsid reptiles survived from the Late Carboniferous into the Permian, followed by pareiasaurian reptiles and the first therapsids, which diversified rapidly toward the end of the period. Cycads and conifers became widespread as the drying climate gradually ended the coal swamps of the Carboniferous. The *Glossopteris* flora dominated plant life in Gondwana. The period ended with the most severe mass extinction in Earth's history, setting the stage for the emergence of dinosaurs of the Mesozoic.

Permian extinction the most severe of the five great extinctions, marking the end of the Paleozoic Era at 252 Ma. Like the four other mass extinctions, the Permian event may have occurred in several phases. Two smaller extinction pulses occurred at 259.8 and 254.1 Ma, marking the end of the Capitanian and Wuchiapingian Ages, respectively. A more extensive extinction dated at 251.9 Ma is generally referred to as the end-Permian extinction.

At least 90% of marine species became extinct, while the terrestrial extinctions were less severe but still estimated to be 75% of species, especially the large herbivores. Most lineages of insects were not severely affected except for the pterygote superorder Palaeodictyopteroidea, which became extinct at about 252 Ma. Among the marine groups that did not survive were the trilobites, rugose corals, blastoid echinoderms, rostroconch mollusks, fenestrate bryozoans, and eurypterids. Among those that survived in only one or two orders were the brachiopods, crinoids, and nautiloids. After the Permian extinction, mollusks came to rival arthropods for dominance in marine environments, and modern corals and bryozoans replaced the Paleozoic types. For the flora, see **Umm Irna.**

Several factors have been suggested as causes, but volcanic eruptions (see **Siberian Traps**) are increasingly stressed as the primary cause, especially because of high levels of carbon dioxide emitted into the atmosphere. There was clearly global environmental degradation, including low levels of oxygen in the oceans, evident in widespread sediments. Other possible contributing causes are global cooling and the disappearance of many nearshore environments as the continents coalesced into Pangaea.

Peronopsis a genus of isopygous trilobites in the order Agnostida and family Peronopsidae. Global distribution, middle to late Cambrian.

Perotrochus a genus of vetigastropod mollusks in the family Pleurotomariidae. One of the few pleurotomariids still extant, *P. quoyanus* is now known only in deep-water. Cosmopolitan, Jurassic to Recent.

Perudyptes a genus of large penguins in the family Spheniscidae. Flightless and adapted like all penguins for diving, *Perudyptes* was about the size of the modern emperor penguin and is one of the earliest definitive penguins known, dated at 42 Ma. Peru, middle Eocene.

Pes plural pedes; the distal part of the hindlimb of bipedal vertebrates, corresponding to the human foot.

Petalichthyida an order of flattened placoderms, probably benthic. They were protected by cranial and trunk shields, and they had a partly ossified skeleton. Australia, Asia, Europe, and North America; Devonian to Carboniferous.

Petalodont dentition teeth that are specially hardened, flat-crowned, and embedded in the palate. Petalodonty is an adaptation for grazing on tough organisms like crinoids, sponges, and other encrusting animals.

Petalodontidae a family of primitive skate-like holocephalic fish in the subclass Chondrichthyes and order Petalodontiformes. Their classification is obscure because they are known primarily from their petalodont teeth. *Belantsea* and *Janassa* are the best-known genera. United States and Europe, Carboniferous to Permian.

Petrocrania a genus of brachiopods in the extant order Craniida and family Craniidae. Calcitic and inarticulate, *Petrocrania* is generally found with its pedicle valve attached, sometimes to other brachiopods. Global distribution, Middle Ordovician to Permian.

Petrolacosaurus **kansensis** the earliest-known diapsid, a species of North American reptiles in the order Araeoscelida, about 16 inches long and insectivorous; Kansas, Late Pennsylvanian, 302 Ma.

Peytoia see **Anomalocarididae.**

Pezophaps solitaria the Rodrigues solitaire, a species of birds in the family Columbidae and extinct subfamily Raphinae. *Pezophaps* ("pedestrian pigeon") is a monospecific genus but is closely related to the dodo. The size of a swan and flightless, *Pezophaps* was endemic to the island of Rodrigues, in the Indian Ocean east of Madagascar. It was discovered in 1691 and was hunted to extinction within a century. Pleistocene to Recent.

Pezosiren portelli "walking sirenian," the earliest-known fully quadrupedal sirenian, placed in the family Prorastomidae with the fully aquatic *Prorastomus*. Hippopotamus-like, it was probably amphibious, and it represents an important transitional stage between fully terrestrial mammals with four legs and fully aquatic mammals with flippers. Jamaica, early Eocene.

Phaceloid of colonial corals, having cylindrical vertical corallites with separate walls, joined together at the base. The long, vertical corallites were cemented together irregularly by horizontal tubuli, and there was no contact in life between the polyps living at the top of the column of corallites.

Phacopida "lens-face," a large and diverse order of trilobites with three suborders

Phacopina (with schizochroal eyes), Cheirurina (holochroal eyes), and Calymenina (holochroal eyes). Global distribution, late Cambrian to the end of the Devonian.

Phacops rana The famous *Phacops rana* has been renamed ***Eldredgeops rana***, and some, but not all, other *Phacops* species have also been renamed. See ***Eldredgeops***.

Phalangeridae an extant family of small marsupials in the order Diprotodontia. They are closely related to the Didelphidae and are sometimes referred to as a type of opossum. Generally arboreal and nocturnal, the phalangerids have diversified into several herbivore-insectivore niches. They appeared in the late Oligocene, spread across Australasia, and are still widespread there. Australasia and Indonesia, Oligocene to Recent.

Phalangiotarbida an order of early arachnids, considered a sister group of the Opiliones but possibly related also to the Acari; Europe and United States, Devonian to Permian.

Phanerorhynchus a genus of chondrostean fish in the family Phanerorhynchidae. About 6 inches long, it is characterized by a long rostrum, large body scales, unjointed, spiny fin rays, and vertical jaw suspension. Europe, Late Carboniferous.

Phanerozoic "visible life," the geologic eon from the beginning of the Cambrian to the present. See also **Geologic Time Scale.**

Phareodus a genus of freshwater osteoglossomorph fish in the family Osteoglossidae. From 6 to 7 inches long, it is known in two species, *P. encaustus* and *P. testis*. North America, Europe, Asia, and Australia; Cretaceous to Eocene.

Phascolarctidae "pouch bears," an extant family of marsupial mammals in the order Diprotodontia. It includes only one extant species, the modern koala (*Phascolarctos cinereus*), but about eight extinct genera are known, including *P. stirtoni*, which became extinct in the late Pleistocene. Arboreal herbivores weighing as much as 50 pounds, the family originated in the late Oligocene and is closely related to the Vombatidae. Australia, Oligocene to Recent.

Phascolonus a genus of herbivorous Australian marsupials in the order Diprotodontia and family Vombatidae. One of several extinct genera of large wombats, *Phascolonus* weighed about 450 pounds. It is known from the middle Pliocene to the middle or late Pleistocene.

Phenacodontidae an early family of herbivorous mammals, possibly ancestral to the later ungulates. The type genus *Phenacodus*, resembling *Hyracotherium* but slightly stockier, was one of the earliest and most primitive of the ungulates. Their size increased from 15 to 120 pounds from the Paleocene to the Eocene. North America and Europe, Paleocene and Eocene.

Phenotype the observable traits of an organism.

Phillipsastreidae a family of generally colonial rugose corals in the order Stauriida and suborder Columnariina. Its corallites did not have separate walls but had radially arranged and sometimes curving septa, resulting in a star-shaped cross-section. Global distribution, Early to Late Devonian.

Phillipsia a genus of small trilobites in the order Proetida and family Proetidae; synonym *Griffithides*. About 2 inches long, it was isopygous, with a large cephalon and pygidium. Not numerous, it was one of the last trilobites. North America, Europe, Australia, and Asia; Early Carboniferous to late Permian.

Philonyx see ***Quadrops.***

Phiomorpha an extant clade of Old World hystricognath rodents. The phiomorphs are known mainly from Africa, but they may have originated in Asia. Middle Eocene to Recent.

Phoberomys a genus of giant rodents in the suborder Hystricomorpha and family Dinomyidae. About the size of a buffalo, almost 10 feet long and weighing up to 1500 pounds, it was one of the largest rodents known. (See also ***Josephoartigasia***.) It had small forelimbs and teeth typical of herbivores and was notable for a long tail which it could use to balance on two feet to look over the vegetation of the swamplands where it lived. Northern South America, known only from the late Miocene.

Phocavis maritimus the earliest-known species of diving birds of the family Plotopteridae. Known only from one specimen found on the Oregon coast. United States, late Eocene, 39 Ma.

Phocidae the true seals, an extant family of pinnipeds in the superfamily Phocoidea. The phocids are probably descended from *Enaliarctos* and possibly related to the ursids. They were earless and overall more specialized for aquatic life than their relatives, the Odobenidae and Otariidae. Global distribution, middle Miocene to Recent.

Pholadomya "hole clam," an extant genus of inarticulate marine bivalves in the superorder Anomalodesmata and order Pholadomyoida, widespread in the Mesozoic. Deep-burrowing and up to 5 inches long, with a shell that gapes open at the posterior end so that the siphon can be partially withdrawn. Late Triassic to Recent.

Pholidophorus a long-lived genus of primitive teleost fish in the order Pholidophoriformes. About 18 inches long, with large eyes and an advanced homocercal tail, it was an efficient predator. One of the earliest teleosts, it had ganoid scales, and its skeleton was partly bone and partly cartilage, linking the holosteans and teleosts. South America, Europe, and Africa; Middle Triassic to Late Jurassic.

Pholidota the pangolins, an order of mammals once distributed globally and dating back to the Paleocene; now extant only in Africa and Southeast Asia.

Phoronida an extant but very small phylum of lophophorates related to brachiopods and bryozoans. They are tube-dwelling vermiforms that filter feed by means of the cilia on a crown of tentacles. From 1 to 20 inches long, they have no hard parts, and there are no undisputed fossil specimens except as trace fossils in the form of the chitinous tubes that they construct as burrows. Living phoronids burrow into both soft and hard substrates. Global distribution, Early Devonian to Recent.

Phorusrhacidae a family of large, flightless carnivorous birds in the order Cariamiformes. Characterized by a large head and neck, with short wings used only for balance, they averaged about 5 feet high. The phorusrhacids lived on the South American continent while it was an island in the early Cenozoic. Probably seizing and killing their prey by battering it on the ground, they were the principal carnivores of the continent until it joined North America in the late Pliocene, when saber-tooth cats, jaguars, and wild dogs migrated southward. The largest of the phorusrhacids, *Kelenken*, found in Patagonia in 2004, grew as high as 10 feet and weighed as much as 500 pounds. South America, early Paleocene to late Pliocene.

Phorusrhacos longissimus a genus of carnivorous birds in the family Phorusrhacidae, notable for a long skull and long jaw with a hooked beak. South America, Miocene.

Phosphatocopina see **Podocopa**.

Phragmocone the chambered part of the shell of a cephalopod, which grew larger as the animal grew older.

Phyletic gradualism a model of evolution that stresses steady, gradual evolutionary change (see **anagenesis**) as the basic mode of speciation; this gradual change is considered to occur throughout the history of the lineage.

Phyllocarida an extant subclass of crustaceans in the class Malacostraca, distinguished by a folded bivalved carapace that covers almost the entire body. It includes three orders

the extinct Hymenostraca (Cambrian) and Archaeostraca (Cambrian to Silurian) and the extant Leptostraca, a small but long-lived group that also appeared in the Cambrian. Most other crustaceans are classified in the Eumalacostraca. Global distribution, middle Cambrian to Recent.

Phylloceras a genus of nektic ammonoids in the order Phylloceratida. The smooth shell, 4–10 inches long, is laterally flattened with no ornamentation. Global distribution, Late Triassic to the end of the Cretaceous.

Phylloceratida a conservative Mesozoic order (or suborder) of ammonoids. Generally smooth or weakly ornamented, they are marked by a complex phylloid suture. The phylloceratids are probably ancestral to the highly diverse Jurassic and Cretaceous ammonoids. They themselves persisted almost unchanged from the Early Triassic to the Late Cretaceous; global distribution.

Phyllograptus a colonial graptolite of the Ordovician in the order Graptoloidea and family Phyllograptidae. They are distinguished by the oval, leaf-like shape of the colony, which was 1 to 2 inches long. Several species are index fossils for the Early Ordovician. Global distribution, Early to Late Ordovician.

Phylloid leaf-like, in the shape of a leaf.

Phyllolepida "leaf scale," an order of small, flattened placoderms, possibly related to the arthrodires. The phyllolepids were freshwater predators with whole-plate armor, a wide mouth, and probably only vestigial eyes. Several genera in three families are known globally from the Early and Middle Devonian, but *Phyllolepis* was the only genus to survive into the Famennian, the final Age of the Devonian. Early to Late Devonian.

Phyllotheca a widespread genus of joint grasses in the order Equisetales; global distribution, Late Carboniferous to late Permian.

Phylogeny the evolutionary history of a biological organism and its relationship to other organisms.

Physalis see **Solanaceae**.

Physeteridae the sperm whales, a family of odontocete whales with one extant genus, *Physeter*. Several extinct genera appeared in the Miocene, and the earliest seems to be *Ferecetotherium*, from Azerbaijan, late Oligocene, 28–23 Ma.

Global distribution, Oligocene? to Recent.

Phytolith "plant stone," a microscopic siliceous structure persisting in plant tissue after the decay of the plant. A common element in the fossil record, phytoliths may identify changes in paleoenvironments, and they may also reveal information about the diet of herbivorous animals. See also **grasses**.

Phytosauria an order of semiaquatic archosaurian reptiles, about 6 feet long, heavily armored, and with an elongated snout; formerly called Parasuchia. An example of convergent evolution, the phytosaurs closely resembled the unrelated crocodiles, but their ancestry is obscure. They were widespread in the northern continents but unknown in Southern Africa, South America, Australia, and Antarctica. Middle to Late Triassic, possibly Early Jurassic.

Pictonia baylei a species of ammonoids in the family Aulacostephanidae. It is an index fossil marking the beginning of the Kimmeridgian Age of the Late Jurassic at 157.3 Ma. France.

Pierolapithecus catalaunicus an ape fossil discovered in 2004 near Barcelona that had the upright posture of human beings, an ape-like body, and fingers like those of chimpanzees. Dated at 13 Ma, it is unique and a possible step in the evolution of ape to human. Only one specimen has been found. Spain, Miocene.

Pikaia an enigmatic genus of small primitive chordates known from the Burgess Shale. It was first considered a polychaete worm or stem-arthropod but was later identified as an early ancestor of chordates; it is now generally assigned to the subphylum Cephalochordata. Laterally compressed and ribbon-shaped, the soft-bodied *P. gracilens* was only about 2 inches long. Canada, middle Cambrian, 508 Ma.

Pilina a genus of monoplacophorans in the family Tryblidiidae; United States and Europe, Ordovician to Silurian.

Pilosa an order of xenarthran mammals that includes the sloths and anteaters. Extinct families of sloths include the **Megatheriidae** and **Nothrotheriidae**, *q.v.* The ancestors of the modern anteaters are less well-known but include the genera *Neotamandua* and *Protamandua*, known from the Miocene and Pliocene. South and North America, Paleocene to Recent.

"Piltdown Man" a sophisticated hoax perpetrated in 1912 by Charles Dawson, who claimed to have discovered a missing link between apes and humans. Although widely questioned, the fraud was discovered only 40 years later when advanced dating techniques showed that the specimen was actually only 50,000 years old. Subsequent examination revealed that it was a deliberate combination of a human cranium with the jaw of an ape, probably an orangutan.

Pinacosaurus a genus of ornithischian dinosaurs in the family Ankylosauridae. *Pinacosaurus* was herbivorous and 16–20 feet long with a spiked tail club. Mongolia, Late Cretaceous, between 80 and 75 Ma.

Pinna a genus of inarticulate bivalve mollusks in the order Pterioida and family Pinnidae. Up to 3 feet long, the equivalved and gaping shell is subtriangular and thin, with radial ribbing and faint concentric growth lines. Global distribution, Carboniferous to Recent.

Pinnipedimorpha a clade of carnivorous marine mammals that includes the ancestors of seals, sea lions, and walruses. See ***Puijila*** and ***Enaliarctos***. Global distribution.

Pinopsida an extant class of cone-bearing gymnosperm trees, the most successful group of gymnosperms still living. The earliest Pinopsida, conifers of the Middle Carboniferous and early Permian which had subcompact cones, may have been the first plants whose seeds could remain dormant for a considerable time before germination. See also ***Araucaria*** and ***Lebachia***. Global distribution, Middle Carboniferous to Recent.

Piranhamesodon pinnatomus a species of unusual pycnodontiform fish. Described in 2018, its dentition suggests that it preyed primarily on other fish rather than on shellfish and sea urchins as most pycnodontiforms did. In addition to numerous irregularly rounded and flattened teeth, *Piranhamesodon* had several scissorlike sharp and curving teeth. It is considered the earliest example of this flesh-tearing dentition in the Actinopterygii. Germany, Late Jurassic, 153–151 Ma.

Pisanosaurus mertii a species of early dinosaur-like archosaurs. Discovered in 1962, it was long considered one of the only Triassic ornithischians on the basis of some similarities in dentition. However, it is now thought to be a dinosauriform, farther back along the line of descent to dinosaurs, perhaps a silesaurid. Known only from a single partial skull and upper jaw, with several disarticulated skeletal parts, *Pisanosaurus* is estimated at 3–4 feet long and 5 pounds. Ischigualasto Formation, Argentina; Late Triassic, 231–226 Ma.

Pisco Formation an important Konzentrat-Lagerstätte on the southern coast of Peru. It is known for the only definitive specimen of the large whale *Livyatan* as well as the aquatic sloth *Thalassocnus* and other well-preserved specimens of whales, penguins, marine crocodiles, and sharks. South America, middle Miocene to middle Pliocene.

Pistosauria an order of marine reptiles in the superorder Sauropterygia. About 10 feet long and noted for a very long neck and skull, they were probably transitional between nothosaurs and the larger plesiosaurs. North America, Europe, and Asia; Early Triassic to Late Cretaceous.

Pithecanthropus an obsolete term, once applied to several hominins that are now classified as *Homo erectus*.

Pituriaspis doylei a genus of jawless armored fish which, along with *Neeyambaspis enigmatica*, constitutes a group called pituriaspids. Known only from the Georgina Basin of western Queensland, the pituriaspids resemble the galeaspids in shape, with a pointed rostrum but with a solid bony headshield with no opening. Their affinity to other agnathans is, however, unknown. Australia, Middle Devonian.

Pityaceae a family of plants of the Carboniferous long thought to belong to the Cordaitales but now assigned to the Pteridospermophyta; global distribution, Early Carboniferous.

Placenticeras a genus of large ammonitid ammonoids in the superfamily Hoplitoidea and family Placenticeratidae. Relatively smooth-shelled, they ranged from 1 to 3 feet high. Global distribution, Late Cretaceous.

Placerias a genus of dicynodont therapsids in the family Kannemeyeriidae or Stahleckeriidae. It was among the largest herbivores of the Triassic and one of the last surviving dicynodonts. From 6 to 11 feet long and weighing between 1 and 2 tons, *Placerias* was beaked and had two strong upper tusks. It spent much of its time in the water, with a lifestyle similar to that of a hippopotamus. It is known principally from dozens of skeletons found at the Placerias Quarry in Arizona. United States, Late Triassic, 220–205 Ma.

Placodermi "plated skin," the earliest class of gnathostome vertebrates, primitive jawed fish of the middle Paleozoic. From a few inches to 30 feet long, they had heavy bony armor covering their head, neck, and sometimes thorax. They were the first fish with true paired pelvic fins, the first evolutionary step toward hindlimbs in the tetrapods. Also, some of the first fish to colonize freshwater environments were placoderms (see **Phyllolepida**). Global distribution, early Silurian to the end of the Devonian.

Placodontia an order of sauropterygian marine reptiles. The placodonts, ranging from 3 to 10 feet long, used their flattened teeth to prey primarily on mollusks. The early placodonts like the iguana-like *Placodus* had only light body armor; later genera, such as *Henodus*, though they were not related to turtles, developed turtle-like armor as a defense against the growing numbers of nothosaurs and plesiosaurs toward the end of the Triassic. Europe, Asia, and Africa; Early to Late Triassic.

Placodus a genus of placodont marine reptiles, the type genus of the family Placodontidae. From 6 to 7 feet long, *Placodus* resembled modern marine iguanas in body structure, with a dorsal row of knobs and heavy gastralia. It subsisted mainly, however, on shellfish, plucking them off the sea floor with its protruding incisors and crushing them with its broad, flattened toothplates. Europe and China, Middle Triassic, 245–235 Ma.

Plagiaulacida an order of small basal multituberculate mammals including chiefly the Allodontidae, Paulchoffatiidae, and Plagiaulacidae. North America, Europe, and Asia; Late Jurassic to Early Cretaceous.

Plagiosauroidea "flat lizard," an enigmatic superfamily of early labyrinthodont amphibians in the suborder Stereospondyli. About 3 feet long, they were characterized by completely cylindrical vertebrae and a very short, wide skull (about 6 inches long and 9 inches wide in *Gerrothorax*). South Africa, South America, and Asia; Early to Late Triassic.

Planktic referring to organisms that do not swim actively, independent of the water current. They may swim weakly but generally drift passively with the current, unable to resist the force of the current. See also **pelagic.**

Planocephalosaurus an early genus of rhynchocephalian diapsid reptiles in the family Sphenodontidae. Only about 8 inches long, it was similar in most other respects to the modern tuatara. North America and Europe; Late Triassic, 210–200 Ma.

Plastomenidae a poorly known clade of softshell cryptodire turtles in the extant family Trionychidae. Plastomenids are known only from the Late Cretaceous (Campanian) to the early Eocene of the United States.

Plastron the hard ventral covering of turtles.

Plateosauria a clade of early sauropodomorph dinosaurs that includes most of those called prosauropods. Late Triassic to Late Cretaceous, 231–66 Ma.

Plateosaurus "broad lizard," a genus of basal sauropodomorph dinosaurs, often referred to as a prosauropod. From 15 to 30 feet long and weighing up to 8000 pounds, it was among the largest of its time. *Plateosaurus* appeared at the end of the Triassic and survived into the Early Jurassic. Central and Northern Europe and possibly North and South America and Africa, 215–196 Ma.

Platybelodon "flat tusk," the most common shovel-tusked gomphothere, a genus of large proboscideans in the family Amebelodontidae. *Platybelodon* was similar to *Amebelodon*, another shovel-tusker. Africa, Europe, Asia, and North America; Miocene.

Platyceratidae a family of cap-shaped archaeogastropods in the suborder Euomphalina. Their conical shell was 2–4 inches high, often curved and with irregular growth. Snail-like, they are notable for a symbiotic relationship since they are found only clinging to crinoids, usually on the calyx. Sometimes found near the anus, they may have been coprophagous, but their place of attachment is marked by a scar in some specimens and even a small hole in others, so that they may have been parasitic. The type genus *Platyceras* is speciose and especially well-known. Global distribution, Ordovician to Jurassic, and possibly later.

Platycrinites a speciose genus of camerate crinoids in the family Platycrinitidae; its suborder is either Compsocrinina or Glyptocrinina. It had a crown up to 3 inches high, composed of large, heavy plates. Its stem, sometimes of alternating thick and thin plates, was long and in most genera twisted. Global distribution, Devonian to Permian.

Platygyra see ***Coeloria.***

Platyhelminthes the flatworms, a phylum of acoelomate organisms that are generally parasites. Having no body cavity, flatworms have relatively simple circulatory, digestive, and respiratory systems. They spread worldwide after developing from free-living organisms, known only as far back as the middle Permian.

Platyostoma a genus of marine gastropod mollusks in the order Euomphalina and family Platyceratidae. It was low-spired, about 1.5 inches high, and the final whorl was the largest. North America and Europe, Silurian to Devonian.

Platypus see ***Ornithorhynchus***.

Platyrrhini an infraorder of anthropoid primates that comprises the New-World monkeys. They are characterized by nostrils that face sideways and by prehensile tails. The Platyrrhini diverged from the Catarrhini in the late Eocene or early Oligocene, but they have remained primarily alike, an example of parallel evolution. South America, Eocene to Recent.

Platysomidae a family of palaeonisciform fish in the suborder Platysomoidei. They are deep-bodied and vertically flattened, with ganoid scales. Global distribution, Carboniferous to Triassic.

Plectronoceras "spur horn," a genus of primitive chambered cephalopods in the subclass Nautiloidea and order Ellesmerocerida. The earliest-known nautiloid *Plectronoceras* is known from only a few specimens and was evidently short-lived. *Plectronoceras* had a tapering conical shell 1 inch high, with several septa and a siphuncle. Its body plan was not so well-adapted to swimming as the orthoconic shells of later nautiloids. North America, late Cambrian.

Plegiocidaris a genus of euechinoids in the order Cidaroida, highly ornamented with a variety of tubercles and prominent ridges between its five sinuous ambulacra. Its robust, ridged primary spines give it the appellation "pencil urchin." Europe, Asia, and Madagascar; Triassic to Cretaceous.

Pleistocene the next-to-last epoch of the Cenozoic Era, generally considered to have begun at 2.6 Ma and lasting to 11,700 years before 2000 A.D.

Plesiadapiformes a paraphyletic suborder of primate-like mammals, appearing in the Cretaceous, diversifying rapidly in the late Paleocene, and then disappearing at the end of the Eocene. The suborder is generally considered to include the families Carpolestidae, Chronolestidae, Micromomyidae, Microsyopidae, Palaechthonidae, Paromomyidae, Picrodontidae, Picromomyidae, and Plesiadapidae. The enigmatic genus *Purgatorius* is also sometimes classed as a plesiadapiform. North America, Europe, Asia, and Africa.

Plesiadapis a genus of small scansorial primates, the type genus of the family Plesiadapidae. It is probably the only primate until *Homo sapiens* to inhabit both the Old and the New World. North America and Europe, late Paleocene to early Eocene.

Plesiobaena antiqua a species of softshell cryptodire turtles in the family Baenidae. It was about 2.5 feet long and had a long tail. Alberta, Canada, Late Cretaceous, 80 Ma.

Plesiobaena putorius see ***Cedrobaena.***

Plesiocidaroida an order of regular echinoids in the subclass Euechinoidea. Poorly known, it is one of the groups of euechinoids that diversified in the Late Triassic after almost all echinoids became extinct at the end of the Permian. Italy and North Africa, Late Triassic, 240–220 Ma.

Plesiolestes a genus of plesiadapiform primates in the family Palaecthonidae; synonym *Torrejonia*. One of the earliest-known primates *Plesiolestes* had a body length of 15 inches. It was arboreal, with long legs, fingers, and toes. North America, early Paleocene, 63–57 Ma.

Plesiomorphy a character shared by an organism with primitive ancestors.

Plesiopithecus teras a species of strepsirrhine primates known from two North African specimens. It had large eyes and a dentition suggesting it may have preyed on grubs in tree bark. These features have led to speculation that it may be related to the aye-aye of Madagascar; see ***Propotto***. Fayum, Egypt; late Eocene or early Oligocene.

Plesiosauridae the earlier of the two families of large marine reptiles in the order Plesiosauria (see **Elasmosauridae**); global distribution, Triassic to Late Cretaceous.

Plesiosauria "near lizard," an order of mainly marine sauropterygian reptiles. Plesiosaurs grew to more than 40 feet long and had longer necks than tails, using their four strong flippers to become especially efficient swimmers. Appearing in the Late Triassic, the plesiosaurs are related to the nothosaurs but directly descended from the pistosaurs. They flourished worldwide in the Jurassic and persisted to the end of the Cretaceous.

Pleuracanthodii see **Xenacanthida.**

Pleural lobes chiefly of trilobites, the lateral segments of the body, on both sides of the thorax; from Greek *pleura*, side or rib.

Pleurodictyum a genus of dome-shaped colonial tabulate corals in the family Favositidae. Its slender polygonal corallites encrusted hard substrates. *Pleurodictyum*

problematicum is usually found with the tubes of the worm *Hicetes* at the base of the colony, evidently built on the tubes and possibly commensal with the worm. Global distribution, late Silurian to Carboniferous.

Pleurodira "side neck," the smaller of the two extant suborders of turtles in the order Testudines. Pleurodires are different anatomically from the cryptodires in several ways because of the lateral flexure of the head, which is withdrawn to the side, in front of one of the forelimbs. Australia, Africa, and South America; Jurassic to Recent.

Pleuromeiaceae a family of small trees 3–4 feet high, lycophytes that may be related to the Lepidodendrales and possibly ancestral to the modern Isoetaceae. They are incertae sedis, however, because of a scarcity of fossil specimens. Global distribution, Carboniferous to Early Triassic.

Pleuronectiform having both eyes on one side of head, characteristic of many flat fish and bottom feeders.

Pleurotomaria a very long-lived genus of Paleozoic sea snails, gastropod mollusks in the extant order Vetigastropoda and superfamily Pleurotomarioidea. It is related to the modern abalone but is characterized by a conical or top-shaped shell, 2–3 inches high, with considerable ornamentation and the typical pleurotomariid indentation in the lip. Known worldwide since the Ordovician, it flourished in the Mesozoic before declining in the Cenozoic. Global distribution, Ordovician to Miocene.

Pleurotomariidae a large and long-lived family of vetigastropod mollusks in the superfamily Pleurotomarioidea. The family appeared in the late Cambrian and flourished through the Paleozoic and Mesozoic. It was the only pleurotomarioid family to survive the end-Cretaceous extinction, declining thereafter with only a few genera still extant. Global distribution, late Cambrian to Recent.

Pleurotomarioidea a superfamily of vetigastropod mollusks. Now known only in a few deepwater genera (see ***Perotrochus***), these marine snails originated in the Ordovician and were widespread in shallow seas in the Mesozoic. Most groups have a slit-like indentation in the outer lip of the aperture and are often referred to as "slit shells." Global distribution, Early Ordovician to Recent.

Pliobates cataloniae a proposed species of hominoid in the family Pliobatidae, described in 2015 as being close to the divergence between lesser and great apes. Dated at 11 Ma, this gibbon-like tree-dweller weighed about 10 pounds and shares several skeletal features with hominids. Spain, middle Miocene.

Pliocene the fifth and last epoch of the Cenozoic Era, from 5.3 to about 2.6 Ma. In the last half of the period, Earth was warmer than it is now, with Arctic forests much

farther north than today. Early hominins had appeared at the end of the Miocene, and many variants are found in Pliocene strata throughout Africa and Asia. The period saw the beginning of the decline of the large mammals of the Miocene, a decline which culminated in the Quaternary extinctions of the late Pleistocene. The Panama land bridge joined the Americas about 3 Ma, resulting in great changes in the animal populations of the two continents (see **Great American Biotic Interchange**).

Pliohippus a North American horse descended from *Merychippus* and ancestral to *Equus*; middle to late Pliocene.

Pliohyracidae the largest family of early hyraxes in the order Hyracoidea. They were mostly small and partly arboreal, but several genera were the size of a small horse. Africa, Eocene to Pliocene.

Pliomera a well-known genus of phacopid trilobites in the family Pliomeridae. It is characterized by a pentagonal glabella; small, raised eyes; up to two dozen thoracic segments; and a small pygidium. Argentina, Norway, Russia, and China; Early Ordovician, 479–472 Ma.

Pliomeridae a family of Ordovician phacopid trilobites in the suborder Cheirurina. Several subfamilies are monophyletic but others are uncertain. Global distribution, Early to Late Ordovician.

Plionarctos a genus of short-faced bears in the extant subfamily Tremarctinae. The earliest tremarctine *Plionarctos* was probably ancestral to *Arctodus* and the other members of the subfamily. North America and Europe, late Miocene to Pleistocene.

Pliopithecus a genus of early hominoid primates in the superfamily Pliopithecoidea. *Pliopithecus* appeared in Asia in the early Miocene and spread into Europe before disappearing about 10 Ma. Although gibbon-like, it is not considered a direct ancestor of the gibbons. See ***Propliopithecus***.

Pliosauroidea a suborder of marine sauropterygian reptiles in the order Plesiosauria. Pliosaurs had a relatively short neck and a massive skull. A 33-foot-long specimen found in the early twenty-first century is the first entire intact skeleton of a pliosaur. It was recovered at Spitsbergen, 800 miles from the North Pole. Europe, Africa, and Australia; Early Jurassic to Late Cretaceous.

Plotopteridae a family of diving birds in the order Suliformes. Large, flightless, wing-propelled swimmers but unrelated to penguins, they are a good example of convergent evolution. Similar to cormorants but 3–7 feet long, they are known around the North Pacific Rim from California to Japan; Eocene to Miocene.

Plotosaurus "swimmer lizard," a genus of mosasaurs in the order Squamata; synonym *Kolposaurus*. A strong swimmer, it was similar to ichthyosaurs but more closely related to turtles. Known only from a complete skull and skeletal fragments found in central California, it is estimated to have grown to as much as 40 feet long. United States, Late Cretaceous, 70–66 Ma.

Pluricarpellatia a genus of flowering aquatic plants in the extant order Nymphaeales. Found in the Crato Formation of Brazil and dated about 112 Ma, it is a basal angiosperm. With flowers, seeds, large leaves, and branching rhizomes, it resembles modern water lilies. Brazil, Early Cretaceous.

Pneumodesmus newmani "air band," a species of diplopod millipedes in the superorder Archipolypoda, known only from one specimen found in 2004. Although incertae sedis and dated variously between 428 and 420 Ma, it is generally considered the earliest-known terrestrial animal because it seems to have an air-breathing mechanism that would function only on land. See also ***Mosineia***. Scotland, late Silurian or Early Devonian.

Poaceae the grasses, in the order Poales; formerly Gramineae. The earliest-known grass fossils go back to the time of the dinosaurs, with phytoliths from grasses known in dinosaur coprolites toward the end of the Early Cretaceous. Changing environmental conditions in the Paleocene may have encouraged the spread of grasses, but the first grasslands seem to have appeared only much later, in the middle Eocene, and then to have evolved in conjunction with the rise of ungulate mammals in the Eocene. Since the Eocene, grasses have spread globally and are the most common of all plants today. See also **Fossoriality** and **Ungulates**. Late Cretaceous to Recent.

Podocarpaceae an extant family of conifer trees in the order Pinales. The fossil record of podocarps is sparse, but see, for example, ***Elatocladus*** and ***Dacrydium***. The podocarps appeared in the Permian and were dominant worldwide in the Mesozoic, with a few genera flourishing in Australasia through the Cenozoic to the present.

Podocopa the principal subclass of ostracods, better-known than the **Myodocopa**, *q.v.* The Podocopa includes the extant orders Platycopida and Podocopida and the extinct order Palaeocopida. (The Bradoriida and Phosphatocopina have traditionally been considered podocopan ostracods but have now been removed and are considered separate groups).

Podokesaurus a poorly known genus of very small saurischian dinosaurs in the superfamily Coelophysoidea. Notable for its small forelimbs, very long hindlimbs, and a long neck and tail, *Podokesaurus* is variously estimated between 3 and 9 feet long. It is known only from two partial specimens, and identification as a genus

separate from *Coelophysis* is debatable, but it is among the earliest dinosaurs found in Eastern North America. Early Jurassic.

Poebrotherium "grass-eater," a genus of even-toed ungulates in the family Camelidae. At 3 feet high, *Poebrotherium* was about the size of a goat, larger than its ancestor *Protylopus*. North America, late Eocene to early Oligocene.

Pogonodon a genus of carnivorous feliform mammals in the family Nimravidae. Weighing 50 to 80 pounds, with 2-inch canines, *Pogonodon* probably hunted from ambush. It was widespread in North America in the Oligocene and may have survived in Eurasia into the Miocene.

Pojetaia a genus of very small, primitive bivalve mollusks in the order Fordillida and family Fordillidae. Suboval, it was less than one-tenth of an inch long. Global distribution, early middle Cambrian.

Polacanthus "many spines," a genus of basal ankylosaurian dinosaurs tentatively placed in the family Nodosauridae and subfamily Polacanthinae. Poorly known from disarticulated body fragments, it was quadrupedal, well-armored with dorsal spines, and estimated to be about 16 feet long. The only species now considered valid is the type species, *P. foxii*. England, Late Jurassic to Early Cretaceous, 150–125 Ma.

Polychaeta see **Annelida** and **Scolecodonts**.

Polydolopidae a family of small South American marsupials in the order Paucituberculata, similar to the extant Caenolestidae but probably not related. South America and Antarctica, middle Paleocene to Oligocene (see also ***Antarctodolops***).

Polygnathidae a family of conodonts in the suborder Ozarkodinina. The family includes several genera that are important as index fossils. Global distribution, Silurian to Late Triassic.

Polygnathus costatus partitus a species of ozarkodinid conodonts in the family Polygnathidae. Its first appearance marks the beginning of the Middle Devonian at 393.3 Ma. Global distribution, to 388 Ma.

Polyodon the paddlefish, an extant genus of cartilaginous acipenseriform fish in the family Polyodontidae. Averaging about 5 feet long, it is notable especially by its paddle-shaped, elongated rostrum. The genus, known for its primitive features, has almost disappeared but is still found in China and the central United States. The Polyodontidae were widespread in Asia and North America from the Late Cretaceous to the early Eocene. Cretaceous to Recent.

Polyphyletic group a group of organisms that are similar in some ways but do not derive from a single common ancestor in the group, so that the name of the group is used only informally. A monophyletic group is a clade consisting of an ancestor and all of its descendants, as opposed to a paraphyletic group, which consists of a common ancestor and some but not all of its descendants. Some paraphyletic groupings are still useful; for instance, the clade Amniota includes the mammals, birds, and reptiles, so that the taxa Mammalia, Aves, and Reptilia are all paraphyletic but are still important groups considered individually. See also **Stem group**.

Polyphyodonty see **Dentition**.

Polyplacophora the chitons, an extant class of marine mollusks known from the Cambrian but with a sparse fossil record; synonym Amphineura. They are characterized by an oval, flattened body covered with a dorsal shell of seven or eight calcareous, slightly overlapping plates. See also ***Wiwaxia***. **G**lobal distribution, Cambrian to Recent.

Polypodiopsida see **Filicopsida.**

Polyprotodont an informal term used for a diverse and widespread grouping of primitive marsupials that arose in the Cretaceous and was succeeded in the Oligocene by the diprotodonts.

Pondaungia a species of small, primitive haplorrhine primates in the family Amphipithecidae; synonym *Amphipithecus*. It was probably frugivorous, similar in some ways to the adapiform primates of North America. Burma, early Eocene.

Porifera the phylum of sponges. Whether the phylum is monophyletic is in dispute, but it is generally considered to date from the late Precambrian, with definitive specimens appearing in the early Cambrian. There are several extant classes of sponges

Hexactinellida, Calcarea, Sclerospongiae (polyphyletic), and Demospongiae. The Stromatoporoidea and the extinct Archaeocyatha, Receptaculitidae, and Sphaeractinoidea are also considered sponges in some classifications. Along with the chambered sphinctozoans and the polyphyletic chaetitids, several of these groups have nonspiculate, calcareous basal skeletons and are referred to as **hypercalcified sponges**, *q.v.*

The simplest multicellular animals, sponges, lack a brain, heart, digestive tract, nerves, or muscles. They filter water through pores in a saclike body, feeding on the small organisms in the water before expelling it. The body support of the Calcarea consists of calcium carbonate, while that of the other classes is of siliceous spicules or the fibrous scleroprotein spongin. Global distribution, late Ediacaran to Recent.

Porocharaceae a family of charophytic algae in the order Charales, probably ancestral to the post-Paleozoic family Raskyellaceae and others; cosmopolitan, Carboniferous to Cretaceous.

Poroxylaceae a monogeneric family of pteridospermous plants formerly assigned to the Cordaitales but now considered progymnosperms or seed ferns; global distribution, Carboniferous.

***Posidonia* Shale** see **Holzmaden**.

Postosuchus "crocodile from Post," a genus of large archosauromorph reptiles, considered a rauisuchian. Most specimens come from the Post Quarry in West Texas, but others have been found across the southern United States. Up to 15 feet long and 4 feet high, *Postosuchus* is variously estimated to have weighed between 600 and 1500 pounds and was one of the dominant predators of the Triassic in the region. It had erect posture, with its legs directly under the body. Its forelimbs were somewhat shorter than the hindlimbs but were robust enough to enable it to walk either bipedally or quadrupedally. United States, Late Triassic, 222–201 Ma.

Pourtalesia an unusual genus of atelostomate euechinoids in the order Holasteroida and family Pourtalesiidae, found only in deepwater locations around the Indian Ocean. Its elongate, bottle-shaped body has a thin test with very small pores and tubercles. Asia, Miocene to Recent.

Praecambridium sigillum a species of small Ediacaran organisms in the phylum Proarticulata and family Yorgiidae. Less than half an inch long, it superficially resembles a trilobite but does not have true segmentation. South Australia, late Ediacaran, 567–550 Ma.

Precambrian Eon the long period of geologic time preceding the Paleozoic Era, up to 541 Ma. There are signs of organic life as far back as 4 billion years and fossils of bacteria as old as 3.5 billion years. The first structurally complex eukaryotes appeared about 1.5 billion years ago, but the first multicellular organisms came much later, around 700 Ma. The last part of the Precambrian, the Ediacaran Period (630–541 Ma), is marked by rapidly diversifying marine animals. See also **Geologic Time Scale.**

Prenocephale a genus of small ornithischian dinosaurs in the family Pachycephalosauridae. About 7 feet long, *Prenocephale* had a thick and slightly domed skull fringed by rows of bony nodules. The flat-headed "*Homocephale*" is probably a juvenile of the genus. Nemegt Formation, Mongolia, Late Cretaceous.

Preservational environment a depositional environment that fosters the preservation of fossils, especially in relation to the degree of acidity in the soil or marine strata, since high acidity tends to dissolve bone and other organic remains.

Priapulida an extant phylum of burrowing marine worms in the clade Scalidophora. The priapulids are characterized by a tubular shape, spines around the mouth, and an extendable, spiny feeding proboscis; some species are tolerant of anoxia and hydrogen sulfide. They range from less than an inch to 15 inches long. Stem-group priapulids are known from Cambrian strata, with the earliest crown-group specimens appearing only in the Late Pennsylvanian. See also ***Ottoia***, ***Selkirkia***, and ***Paraselkirkia***. Global distribution, Cambrian to Recent.

Pricyclopyge a genus of small deep-ocean asaphid trilobites in the family Cyclopygidae. Noted for a broad glabella and very large holochroal eyes, it may have swum upside down. Europe and Asia, Early to Late Ordovician.

Primates an order of generally bipedal mammals with two suborders, **Strepsirrhini** and **Haplorrhini**, *q.v.*

Primelephas a genus of primitive elephants with four tusks in the subfamily Elephantinae. Similar to the gomphotheres, it was one of the first elephants, probably ancestral to the Mammutoidea and to modern elephants. Africa, Miocene to Pliocene.

Primicaris a genus of arthropods in the family Parvancorinidae, first known in the Chengjiang biota and later found also at the Marble Canyon site of the Burgess Shale. See

Misszhouia. China and Canada, early to middle Cambrian, 515 to 508.

Primitiopsis a genus of ostracods in the order Palaeocopida. It is dimorphic and lived primarily in the deep subtidal zone. Cosmopolitan, Late Devonian and Silurian.

Primitive features characteristics of an organism that are relatively close to those of its ancestors, as opposed to advanced features.

Prioniodontida a clade of conodonts with composite teeth, including the suborders Ozarkodinina, Prioniodinina, and others; global distribution, Early Ordovician to Triassic.

Prionocyclus a genus of ammonoids in the order Ammonitida and family Collignoniceratidae. Ranging in size between 2 and 4 inches, several species are index fossils for the Turonian Age of the Late Cretaceous. Global distribution, 94–90 Ma.

Prionosuchus a genus of very large temnospondyls in the family Archegosauridae. The largest amphibian at an estimated 30 feet long, it is known from two partial specimens. Brazil, middle Permian.

Priscacara a genus of freshwater actinopterygian fish in the extant family Cichlidae. Of medium size, it is characterized by a flattened oval body and spiny dorsal, anal, and ventral fins. United States, early to late Eocene.

Priscansermarinus "ancient sea goose," a monospecific genus of crustacean arthropods similar to the modern gooseneck barnacle and classified in its order, Pedunculata. *P. barnetti* is known only from the Burgess Shale and is considered the earliest-known barnacle. Canada, middle Cambrian, 508 Ma.

Priscomyzon riniensis a species of agnathan vertebrates in the order Petromyzontiformes. The earliest-known lamprey-like vertebrate *Priscomyzon* is dated 30–40 million years earlier than other basal lampreys. Known only from one complete body fossil, it was about 2 inches long and had a large, circular mouth ringed with teeth. South Africa, Late Devonian, 360 Ma.

Pristerodon a genus of dicynodont therapsids. About 2 feet long but only a few inches high, the herbivorous *Pristerodon* seems to be one of the first animals able to hear airborne sounds, as opposed to vibrations in the ground; the type species is *P. mackayi*. Southern Africa and India, late Permian.

Proailurus a genus of catlike carnivores, close to the ancestry of the Felidae, probably ancestral to *Pseudaelurus*. About the size of a lynx but with slender limbs and a long tail, it was partly arboreal. Europe and Asia, late Oligocene to Miocene.

Proanura a suborder of amphibians ancestral to the modern order Anura, the frogs. A very sparse fossil record leaves the phylogeny questionable**:** the only recognized proanuran is *Triadobatrachus*, an Early Triassic amphibian from Madagascar.

Probactrosaurus a genus of Cenomanian ornithischian dinosaurs, one of the smallest and earliest hadrosaurs. About 18 feet long and weighing up to a ton, it was principally quadrupedal, with long and slender forelimbs. *Probactrosaurus* was similar in several ways to *Iguanodon*, the ancestor of the hadrosaurs, but with a thumb spike and weaker forelimbs. It was probably not directly related to *Bactrosaurus*. China, Late Cretaceous, 96–88 Ma.

Probainognathus "advanced jaw," a monospecific genus of small cynodont therapsids in the family Probainognathidae, probably related to the Chiniquodontidae. Carnivorous and the size of a very small dog, *P. jenseni* is one of the earliest therapsids to have a squamosal-dentary jaw joint similar to the typical mammalian structure. Argentina and Brazil, Late Triassic, 235–220 Ma.

Probathyopsis a basal uintathere, a small genus of early dinoceratan ungulates, closely related to the Asian *Prodinoceras*; United States, late Paleocene to early Eocene.

Probelesodon a genus of early cynodonts in the family Chiniquodontidae. The size of a small dog, it is one of the larger chiniquodontids. South America, Middle to Late Triassic.

Proboscidea an order of mammals that originated in Africa in the early Eocene and achieved nearly global distribution by the middle Miocene. The earliest proboscideans, such as *Moeritherium*, were trunkless, but Oligocene species such as *Paleomastodon* had a rudimentary trunk and short tusks. The order includes the two surviving species of elephants as well as the extinct mammoths, gomphotheres, deinotheres, and possibly the desmostylians.

Procaviidae the modern family of hyraxes, known principally from Africa, where some of their ancestors in the Pliohyracidae evolved into sirenians and elephants; Africa, Europe, and Asia; Miocene to Recent.

Proceratops see **Ceratopsia**.

Procolophonidae a family of mostly small fossorial reptiles in the suborder Procolophonia. Related to the Pareiasauria, they were formerly included in the paraphyletic order Captorhinida. The early procolophonids were about a foot long and mainly ate insects and small vertebrates. Later genera are less well-known but were larger and probably herbivorous, with broader, platelike teeth. They survived the end-Permian extinction and diversified very rapidly in the Early Triassic. Global distribution including Antarctica, late Permian to Late Triassic.

Proconsul a genus of arboreal hominoid primates in the family Proconsulidae. About the size of a modern baboon and possibly ancestral to *Propliopithecus* and later primates, including humans, *Proconsul* was sexually dimorphic and bore characteristics of both monkeys and apes. The four named species differ mainly in body size, the specimens ranging from 10 to 150 pounds. Kenya and Uganda, early Miocene, 23–25 Ma.

Procoptodon a genus of short-faced kangaroos in the family Macropodidae and extinct subfamily Sthenurinae. The genus includes the smallest of the Sthenurinae, *P. gilli*, while *P. goliah* was about the same size as *Sthenurus*, weighing more than 500 pounds. They probably moved more slowly than modern kangaroos. Australia, Pliocene to late Pleistocene.

Procyonidae a family of mammals in the superfamily Musteloidea. The family includes principally the raccoons, coatis, and kinkajous. Generally very long-tailed and slender except for the raccoon, they are omnivorous. The procyonids are probably descended from the early Miocene European *Broiliana*; they were widespread in North America from the early Miocene. Procyonids such as *Cyonasua* began to appear in South America at the end of the Miocene. North and South America and possibly Europe, early Miocene to Recent.

Procynosuchus "before dog-crocodile," a genus of basal cynodont therapsids in the family Procynosuchidae. Cat-sized, it was quadrupedal and probably semi-aquatic; it was notable for a very primitive dentition and a long tail. Europe and Africa, Late Permian.

Prodeinotherium a genus of proboscideans in the family Deinotheriidae. Possibly a descendant of the poorly known *Chilgatherium*, it was about 9 feet high at the shoulder and had lower jaw tusks curving down and backward. Europe, Africa, and Asia; late Oligocene to middle Miocene.

Prodinoceras a genus of basal uintathere ungulates in the order Dinocerata. *Prodinoceras* was about 10 feet long and very similar to *Probathyopsis* of North America. Mongolia, late Paleocene.

Prodryas persephone a species of lepidopterans in the family Nymphalidae, a butterfly known from a single, unusually well-preserved specimen found in the Florissant Fossil Beds. About an inch wide, the specimen shows the wing venation and even the original color patterns. United States, late Eocene.

Productida an order of late Paleozoic articulate brachiopods in the class Strophomenata. The productids were a very diverse order containing a wide range of shapes, generally distinguished by concave-convex shells and by spines on the surface. Global distribution, Ordovician to Triassic.

Proetida an order of generally small trilobites, very similar to the Ptychopariida; both orders are included in the proposed subclass Librostoma. Characterized by a narrow rostral plate and a high, sometimes pitted glabella, they were generally less than an inch long. The only order of trilobites to survive the Devonian extinction, the Proetida, diversified and persisted through the Carboniferous and Permian, finally disappearing from the fossil record shortly before the end-Permian extinction. Global distribution, Early Ordovician to Permian.

Profallotaspis one of the earliest trilobites, a genus of redlichiid trilobites in the family Fallotaspididae. Russia and United States, early Cambrian, 525 Ma.

Proganochelys a genus of stem-turtles in the order Testudines; synonym *Triassochelys*. Dated at 210 Ma, it is the oldest turtle found with a complete shell, carapace, and plastron. It was different in several ways from modern turtles; about 3 feet long, it had a spiked tail ending in a club and was probably mainly terrestrial. Europe and Asia, Late Triassic.

Proganosauria see **Mesosauria.**

Prognathodon a genus of squamate reptiles in the family Mosasauridae; synonym *Brachysaurus*. Several species of these large mosasaurs, ranging from 20 to more

than 40 feet long, were widespread at the end of the Cretaceous, preying on fish, ammonoids, other shellfish, and turtles. Skulls and teeth from phosphate deposits near Khouribga, Morocco, are well-known as commercial specimens. Two almost complete specimens from Canada show fins and stomach contents, including a 5-foot-long fish. *Prognathodon* is similar to G*lobidens* in its shape and in a robust skull, and its teeth also are specialized for crushing shellfish, although sharper pointed than the blunt teeth of *Globidens*. North America, Eurasia, Africa, and New Zealand; 71–66 Ma.

Progymnosperms a group of woody, spore-bearing plants intermediate between ferns and gymnosperms; global distribution, Middle Devonian to Mississippian.

Prokennalestes a poorly known genus of basal eutherian mammals tentatively placed in the order Leptictida. With three named species, it is considered a possible ancestor of *Kennalestes* but is known only from fragmentary skull and dental remains. China, Early Cretaceous, 120 Ma.

Prolacertiformes see **Protorosauria**.

Prolecanitida one of the longer-lived and most speciose orders of ammonoids, with more than 1200 species. Discoidal or thinly lenticular, they are notable for the increasing complexity of their suture from the Devonian to the Permian. Global distribution, Late Devonian to Late Triassic.

Promicroceras a small genus of ammonoids in the order Ammonitida and family Eoderoceratidae. Distinguished by strong ribbing and small spines, it is one of the common fossils of the Sinemurian stratum on the Dorset coast, between 199 and 192 Ma. England, Early Jurassic.

Promissum pulchrum a species of conodonts in the suborder Prioniodinina. One of the few known fossil imprints of the animal and the largest known at 16 inches long. Soom Shale, South Africa; Late Ordovician.

Promyalina a genus of bivalves in the order Myalinida. A disaster taxon, it was one of the bivalves that survived the Permian extinction and flourished briefly in the Early Triassic, often found with *Claraia*. Cosmopolitan, Permian to Middle Triassic.

Pronghorn see **Antilocapridae**.

Pronucleolites see **Nucleolitidae.**

Propalaeotherium a genus of very small perissodactyl mammals at first classified in Palaeotheriidae but in 2004 placed in Equidae. It was found in the Messel Shale Pit in 1849 and later across Europe and in China. A forest browser on leaves and berries (found with its stomach contents), it stood 1–2 feet high at the shoulder and

weighed only about 22 pounds. Hoofless, it had nail-like hooflets at the ends of the toes, four on the manus and three on the pedes. Europe and Asia, Eocene.

Proplebeia dominicana a species of stingless bees, hymenopteran insects in the family Apidae, found in amber deposits in the Dominican Republic. Its successfully reconstituted and copied DNA, 40 million years old, is the oldest yet recovered for study. Caribbean, late Eocene to Miocene.

Propliopithecus a genus of early anthropoid primates in the family Pliopithecidae, possibly ancestral to the early hominins. Only 1.5 feet long and with stereoscopic vision, it was more advanced than the earliest primates. It was closely related to the early Oligocene *Aegyptopithecus* and was probably ancestral to *Pliopithecus*. North Africa, middle to late Oligocene.

Propotto leakeyi a species of strepsirrhine primates long thought to be a fruit bat in the family Pteropodidae but now identified as a new primate species. Known from teeth and partial jaws dated between 23 and 16 Ma, *Propotto* may have used its protruding incisors to bore into tree bark, as do the aye-ayes of Madagascar. The scarcity of fossils, especially of the skull and manus, leaves this possibility unresolved. Kenya, early to middle Miocene.

Prorastomidae a family of primitive sirenians, possibly ancestral to the modern dugongs and manatees. Known only from two Jamaican specimens, the partly terrestrial *Pezosiren* of the early Eocene and the fully aquatic *Prorastomus* of the middle Eocene.

Prorichthofenia an unusual genus of reef-forming strophomenate brachiopods in the order Productida and family Richthofeniidae. It is characterized by a conical, horn-shaped pedicle valve, with the upper valve acting as a lid covering the cone. United States and Europe, middle to late Permian.

Prorubidgea see ***Aelurognathus*.**

Prosaurolophus a genus of duckbilled dinosaurs in the subfamily Saurolophinae. Medium-sized hadrosaurids, they were about 30 feet long and had a prominent crest above the eyes. North America, Late Cretaceous, 76–73 Ma.

Prosauropods an informal term for the earliest sauropodomorphs, herbivorous theropod dinosaurs evolving at the end of the Middle Triassic. Prosauropods developed and spread rapidly, and the large *Plateosaurus* and others survived the Triassic extinction, followed by *Anchisaurus* and other sauropodomorphs in the Early Jurassic. The Sauropoda themselves, which included the largest of all dinosaurs, spread worldwide in the Cretaceous. See also ***Herrerasaurus***. Middle Triassic to Cretaceous.

Proscorpius osborni an early species of chelicerates in the class Arachnida and order Scorpiones. Known from several fragmentary specimens, *P. osborni* was probably aquatic. United States, late Silurian or Early Devonian, 420–416 Ma.

Prosimii see **Strepsirrhini.**

Protamandua see **Pilosa.**

Protarchaeopteryx robusta a species of coelurosaurian theropod dinosaurs in the clade Oviraptorosauria. Known from only one specimen, it was probably flightless although it may have been semiarboreal, with long, birdlike legs and true feathers on the body, wings, and tail. More than 3 feet long, it was larger and more primitive than *Archaeopteryx* but lived 10 million years later. *Protarchaeopteryx* is one of several feathered dinosaurs in the Jehol biota. China, Early Cretaceous, 125 Ma.

Protaspis the earliest stage (hatching ontogenetic phase) of larval development in trilobites; see also **holaspis** and **meraspis**.

Protelotherium see ***Achaenodon***.

Proteroctopus a monospecific genus of cephalopods tentatively placed in the family Palaeoctopodidae. Known from only one specimen found at La Voulte-sur-Rhône, *P. ribeti* will be the oldest-known octopus if it is confirmed as one. France, Middle Jurassic.

Proterosuchidae a family of reptiles, probably paraphyletic but including basal archosaurs. When most large therapsids became extinct at the end of the Permian, the proterosuchids became the largest carnivores and flourished at the beginning of the Triassic; in the Middle Triassic, they were replaced by phytosaurs and crocodilians. Global distribution except North America, late Permian to Middle Triassic.

Proterosuchus a genus of large archosauriform reptiles in the family Proterosuchidae; synonym *Chasmatosaurus*. A basal archosaur, *Proterosuchus* grew up to 7 feet long with long jaws, one of the largest land reptiles of its time. In overall appearance it was similar to modern crocodiles except for its distinctive hooked premaxilla, hanging down over the tip of the snout and bearing small teeth. It was first found in the Karoo Basin of South Africa and is now known also from China; Early Triassic, 252–250 Ma.

Proterotheriidae a diverse family of horselike South American ungulates in the order Litopterna. The proterotheres arose in the Paleocene and flourished in the Eocene before declining in the Miocene. Most genera became extinct in the Pliocene at about the time that true horses arrived in South America; one genus, however, survived in Argentina and Uruguay into the Pleistocene.

Protichnites see ***Diplichnites***.

Protists an informal group of unrelated simple, eukaryotic organisms that are not animals, plants, or fungi; they are microscopic and chiefly aquatic.

Protoavis a contentious specimen with a birdlike skull and other birdlike features. Dated at 225 Ma, it has been proposed as an early avian evolutionary branch from the time of the earliest dinosaurs. However, since it is known only from disarticulated and unassociated fragments found at two sites in Texas, its reconstruction is questionable. The tentative reconstruction indicates an animal 1–2 feet long. Although it is unclear whether it had a true wishbone, *Protoavis* seems unlikely to be ancestral to modern birds. United States, Late Triassic.

Protoceratidae a long-lived family of herbivorous artiodactyl ungulates, variously considered tylopods or ruminants. Up to 6 feet long, the protoceratids resembled deer and elk, with a broad, moose-like snout. The males developed a wide variety of horns, usually two or four; the late genus *Synthetoceras* is notable for a pair of long rostral horns above the nose as well as a pair of horns at the back of the head. They flourished from Canada to Texas from the Eocene to the middle Miocene. North America, middle Eocene to early Pliocene.

Protoceratopsidae a family of ornithischian dinosaurs in the suborder Ceratopsia, less advanced than the Ceratopsidae. They were herbivorous, with the characteristic ceratopsian neck frill and large skull, but only up to 9 feet long. One of the many specimens of the type species *P. andrewsi* is preserved with its jaws clamped on the arm of a velociraptor. Known only from Northern China and Mongolia, Late Cretaceous, 84–72 Ma.

Protocetus a genus of archaeocete cetaceans in the family Protocetidae, one of the earliest oceangoing whales, fully aquatic and bearing only vestigial limbs that probably could not have supported its weight on land. Like the deep-ocean *Rodhocetus, Protocetus* had unfused sacral vertebrae, so that it could use its tail efficiently for propulsion in the water. In addition, it had the advanced character of vestigial hindlimbs unattached to the backbone. Egypt, middle Eocene.

Protoconodonts an obscure group of small animals that may be either the earliest conodonts or a stem group of Chaetognatha. They seem at least quite different from the euconodonts. Cosmopolitan, late Precambrian to Early Ordovician.

Protodonata see **Meganisoptera.**

Protoeumalacostraca an obscure group of early crustaceans that are thought to be the stem group of the subclass Eumalacostraca, which includes most of the living crustaceans. The eumalacostracans appeared in the Devonian, but their predecessors remain in doubt.

Protohertzina a genus of protoconodonts, probably the grasping spines of chaetognaths. It is one of the earliest of the "small, shelly fossils" and one of the earliest examples of predation. Global distribution, early Cambrian, 540–520 Ma.

Protopteridales an order of fernlike plants in the class Polypodiatae. Now considered to be related to the Rhyniales, they are eusporangiate, producing sporangia at the edges of their leaves, and either herbaceous or woody. Cosmopolitan, Devonian.

Protopteryx fengningensis a species of primitive enantiornithean birds. Well-feathered, it was about 4 inches long, excluding its two long tail feathers. Although its teeth are similar to those of the earlier *Archaeopteryx*, it was a much stronger flyer and had several skeletal features closer to modern birds, including an alula on the forewing. China, Early Cretaceous, 131 Ma.

Protorohippus a genus of early horses in the family Equidae. Known from several almost complete skeletons, it stood about a foot high and had four toes on its forefeet and three on its hindfeet. Western United States, early Eocene, 52 Ma.

Protorosauria an order of archosauromorph reptiles that flourished in the Triassic; synonym Prolacertiformes. They generally had very long necks and short bodies (see ***Tanystropheus***). Some families, such as the Tanystropheidae, are 15 to 20 feet long, while the Drepanosauridae are only 1–2 feet long. The Protorosauridae of the late Permian, which were about 7 feet long, are the earliest-known archosauromorphs. South America, Europe, and Asia; late Permian to Late Triassic.

Protorothyrididae a family of anapsids that includes the earliest reptiles; see ***Hylonomus*** and ***Paleothyris***. North America and Europe, Late Carboniferous to middle Permian.

Protorthida an order of brachiopods in the class Rhynchonellata. It contains two superfamilies. The smaller, the Protorthoidea, appeared in the early Cambrian and became extinct in the Early Ordovician. The larger, the Skenidioidea, diversified worldwide from the Early Ordovician to the Silurian, disappearing only in the Late Devonian.

Protosalvinia a genus of early land plants. Probably a liverwort, it is similar to some phaeophytes (brown algae) but is generally considered one of the earliest bryophytes. It is known from several Late Devonian specimens found in North and South America.

Protosirenidae a monogeneric family of aquatic mammals in the order Sirenia. Like their descendants the manatees, the protosirenians inhabited temperate to tropical waters. *Protosiren* had hindlimbs, which have disappeared in the modern species. The type species of the genus is *Protosiren fraasi*; see also ***Pezosiren***. United States, Europe, and Asia; Eocene.

Protosuchia a group of small- to medium-sized archosaurian reptiles in the superorder Crocodylomorpha. About 3 feet long, they were slender and terrestrial; global distribution, Late Triassic to Early Cretaceous.

Protosuchus a genus of basal crocodylomorphs that appeared near the boundary of the Triassic and Jurassic. Primarily terrestrial, *Protosuchus* was 3 feet long and moderately armored, and its hindlimbs were somewhat longer than its forelimbs. North America and Africa, Early Jurassic.

Prototaxites an enigmatic genus of large, mid-Paleozoic treelike structures. Estimated to be as much as 3 feet in diameter and 26 feet high, they were named "early yew" because of the long, intertwined tubes that formed the trunk, resembling the proto-vascular structure of other early plants such as the Calamitales or Nematophyta; now considered probably fungal or algal. North America, Europe, and Saudi Arabia; Late Silurian to Late Devonian, 420–370 Ma.

Prototheria an obsolescent term for a subclass of mammals that now includes only the order Monotremata; Late Triassic to Recent.

Protungulatum a genus of early ungulate mammals, considered a nonplacental eutherian, probably related to the arctocyonids. Rat-sized, *Protungulatum* had a distinctive foot structure and crushing molars designed for eating plants. North America, Late Cretaceous to Paleocene.

Protura "first tail," an extant order of very small soil-dwelling and insect-like animals in the phylum Hexapoda and class Entognatha. Less than 2 mm long and eyeless, they have no antennae or pigmentation; they are characterized by six legs, a cylindrical body, and a conical head. Although their fossil record is very sparse, they are thought to go back perhaps to the Early Devonian.

Protylopus a genus of even-toed ungulates in the family Camelidae. One of the earliest camelids, it was about the size of a rabbit. United States, middle Eocene.

Protypotherium an early genus of South American notoungulate mammals in the suborder Typotheria and family Interatheriidae. The rodent-like *Protypotherium* was about a foot long, with long limbs and clawed feet. Southern South America, Paleocene to late Miocene.

Proximal generally referring to a body part of a bilaterian animal that is closer to the center of the body than a distal part. In plants, referring to an area near a point of attachment.

Prozostrodontia a clade of cynodonts including mammals and early mammaliaforms such as the Tritheledontidae and Tritylodontidae.

Psammodontidae a family of holocephalic fish. Characterized by bradyodont dentition consisting of rectangular toothplates in two rows meeting at the midline. North America and Europe, late Devonian to late Permian.

Psammosteidae a family of heterostracan fish in the class Pteraspidomorphi. With a round and flattened body, they ranged in size from the early genus *Drepanaspis* (about 1 foot long) to some at the end of the Devonian that were 6 feet long. They were the only heterostracans to survive the Frasnian extinction but were finally extinguished in the Hangenberg Event at the end of the Famennian Age. Global distribution, Early to Late Devonian.

Psarolepis an enigmatic early genus of lobe-finned fish, perhaps a basal osteichthyan, close to the common ancestry of sarcopterygians and actinopterygian. It exhibits a combination of osteichthyan and non-osteichthyan gnathostome characters. China, dated as early as 418 Ma, at the beginning of the Devonian.

Psaronius a genus of tree ferns in the extant order Marattiales. The name originally referred to only the stem. Growing more than 30 feet high, *Psaronius* had a trunk as large as 3 feet in diameter at the base. It is notable for the structure of its trunk, which consisted of many thin roots intertwined with stems, somewhat similar to the manner of *Tempskya*. The leaves grew in a crown at the top of the trunk and are known mainly as the form genus *Pecopteris*, with the leaves of some species classified in the form genus *Sphenopteris*. North America, Europe, and Asia; Late Carboniferous to late Permian.

Pseudaelurus a genus of Miocene mammals in the family Felidae, the first felid to appear in North America. Early species were the size of a domestic cat, while later ones reached the size of a cougar. North America, Europe, and Asia; early to late Miocene.

Pseudoborniales an early order of sphenopsid plants in the class Equisetopsida, growing to 60–75 feet; cosmopolitan, known only from the Late Devonian.

Pseudocidaris a genus of sea urchins, Mesozoic euechinoids in the family Hemicidaridae. The species *P. mammosa* is well-known for its bulbous, club-shaped spines. Europe, Africa, and Asia; Middle Jurassic to Early Cretaceous.

Pseudolagosuchus see ***Lewisuchus***.

Pseudosuchia a clade now considered to include living crocodilians as well as the reptiles that arose in the Early Triassic and dominated the terrestrial carnivorous niches of the Late Triassic. All except the Sphenosuchia and Crocodyliformes were extinguished in the Triassic extinction. Cosmopolitan, Triassic to Recent.

Psigraptus jacksoni a species of anisograptid graptolites, notable for specimens of three-dimensional pyritized remains of zooids. The specimens show, however, no tentacles or other morphological details. Australia and Korea, Early Ordovician.

Psiloceras spela group a group of smooth ammonitid ammonoids in the family Psiloceratidae. Its first appearance marks the beginning of the Early Jurassic at 201.3 Ma. Austria.

Psiloceratidae a family of ammonoids in the order Ammonitida, probably descended from the Ussuritidae. Psiloceratids generally had a smooth surface or blunt ribbing. Cosmopolitan, Early Jurassic to Late Cretaceous.

Psilophyton a genus of fernlike tracheophytic plants in the class Trimerophytopsida and family Psilophytaceae. Among the first vascular plants, they grew from underground rhizomes, with naked branches and a spore-producing structure at the tips of branches. *Psilophyton forbesii* is the largest known at about 2 feet, but most were 1 foot high. North America, Europe, and Asia; Late Silurian to Late Carboniferous.

Psilophytopsida see **Trimerophytopsida**.

Psittacosaurus a speciose genus of Asian ceratopsian ornithischian dinosaurs in the family Psittacosauridae. The most common dinosaur in the Jehol biota, *Psittacosaurus*, includes more species than any other dinosaur genus and is also one of the most completely known dinosaur genera, known from several complete skeletons and hundreds of individual specimens. *Psittacosaurus* was bipedal, generally 6–7 feet long, and had a large, parrotlike beak. Early in the Cretaceous, probably around 130 Ma, the psittacosaurids split off from the neoceratopsian branch, which led to the familiar horned and frilled ceratopsians of the Late Cretaceous. See also ***Liaoceratops***. China, Mongolia, and Siberia; Early Cretaceous, 123–100 Ma.

Pteranodon "toothless wing," a genus of large pterosaurs in the suborder Pterodactyloidea. They were edentulous, with a large beak and a large cranial crest, and the largest species had a wingspan up to 23 feet. They are especially well-known, from more well-preserved specimens than any other pterosaur. North America and Europe, Late Cretaceous, 86–84 Ma.

Pteraspidomorphi a class of primitive agnathans, jawless bottom-dwelling fish. They were mostly marine and heavily armored, especially around the head; they are sometimes described as having an exoskeleton in the form of plates of acellular bone. Early genera of the Ordovician were small, just a few inches long, while some in the latest family, the Psammosteidae, grew up to 6 feet long. Cosmopolitan, late Cambrian? to Late Devonian.

Pteraspis "wing shield," a genus of small, jawless fish-like vertebrates in the subclass Heterostraci and order Pteraspidiformes. It was finless except for small

winglike protrusions at the sides of the shield over the gills, which may have aided in swimming. It also had a striking medial dorsal spine extending backward from the wide shield that protected the forward half of the body. The rest of the 7-inch-long body was covered by small scales. Europe and possibly Brazil, Early Devonian.

Pterichthyodes a genus of freshwater antiarch placocoderms in the family Asterolepidae. Distinguished by jointed winglike appendages extending outward on both sides of the head, it had a heterocercal tail fin and eyes on top of the headshield. Up to a foot long, it had heavy anterior armor and scales on the posterior, differing from its cousin *Bothriolepis*, which was posteriorly naked, with no scales. It may have used its pectoral appendages to pull itself along the bottom. Known only from Scotland, Middle Devonian.

Pteridinium a genus of enigmatic Ediacaran organisms, probably related to *Ernietta*. Incertae sedis, it seems to have some metazoan features and a trilobed structure similar to that of *Swartpuntia* except that its surface resembles a fern leaf; it has no visible organs or appendages. Australia, Namibia, and Russia; late Ediacaran, 560–540 Ma.

Pteridophyta see **Filicopsida.**

Pteridospermatophyta the seed ferns, a large extinct group of gymnosperms similar to tree ferns except that they bore seeds and pollen-bearing structures on the fronds. Currently eight orders are recognized: Calamophytales, Callistophytales, Caytoniales, Gigantopteridales, Glossopteridales, Lyginopteridales, Medullosales, and Peltaspermales. Some similar plants survived to the Eocene, but the relationship is unclear. The seed ferns have also been called Cycadofilicales and sometimes Pteridospermae. Global distribution, Late Devonian to Cretaceous, but especially important part in Carboniferous floras.

Pteriidae a family of unusually shaped marine bivalves in the order Ostreida or Pterioida. Medium-sized, they are called winged oysters because of their inequilateral and inequivalved shells, with unequal wings extending at a sharp angle from a long, straight hinge. The surface is often rough, with fine radial and concentric ornamentation. Global distribution, Late Ordovician to Recent.

Pterinea a genus of marine bivalves in the order Ostreida and family Pterineidae. The valves are unequal and asymmetrical, with a wide hinge line and fine, concentric growth lines. About 1.5 inches long, it had two unequal muscle scars. Global distribution, Late Ordovician to Late Carboniferous.

Pterobranchia an extant class of small, wormlike colonial animals in the phylum Hemichordata. Phylogenetic analysis indicates that they are related to the graptolites, but they differ in morphology and habits. The benthic pterobranchs usually secrete tube-stalks which they extend to filter feed. Families are Atubaridae,

Cephalodiscidae, and Rhabdopleuridae. Global distribution, early Cambrian to Recent.

Pterodactyloidea a large suborder of flying archosaurs in the order Pterosauria, generally tail-less and much larger than the basal rhamphorhynchoid pterosaurs of the Late Triassic. Several later genera were toothless; many had large crests, and their wingspan ranges from a few inches to as much as 40 feet (see ***Quetzalcoatlus)***. Cosmopolitan, Middle Jurassic to Late Cretaceous.

Pterodactylus "finger wing," the type genus of flying pterosaurs of the suborder Pterodactyloidea; Europe and Africa, Late Jurassic, 151–149 Ma.

Pterodaustro a genus of pterodactyloid pterosaurs in the family Ctenochasmatidae. Known from more than 700 specimens, *Pterodaustro* was a medium-sized pterosaur with a wingspan of 7–8 feet and an extremely elongated skull. The skull was more than a foot long, 90% of it in front of the eyes. The upper and lower jaws curved upward to a point, the lower jaw being two inches deep and containing several hundred long, comb-like teeth that were evidently used to filter planktic prey. Argentina and Chile, Early Cretaceous, 105 Ma.

Pterosauria an order of ornithodiran archosaurs distinguished by the leathery membranes stretched between extremely elongated fingers that enabled them to glide or soar. They are traditionally divided into two suborders, the "rhamphorhynchoids" and the Pterodactyloidea, but only the latter is monophyletic. Beyond this two-part division, the phylogeny of the dozens of families of pterosaurs is hotly disputed. They varied widely, with a wingspan ranging from a few inches to as much as 45 feet. Pterosaurs were carnivorous and especially piscivorous, and many families were toothless.

They were not dinosaurs and not birds but evolved along with dinosaurs from a common ancestor in the Late Triassic. Some consider them closely related to dinosaurs because of a simple-hinge ankle structure, but their origins are too poorly known to be sure. Because their bones were birdlike — thin-walled and slender — the fossil record is less complete for pterosaurs than for most archosaurs. Their eggs are extremely rare, but several discoveries since 2004 have shown that the parents may have buried eggs; whether they were altricial or not is also unclear.

No feathers are known in pterosaurs, but several species had a furry covering of pycnofibers, a hair-like material analogous to mammalian hair. The exact shape of their wings and their mode of flying is still unclear. Some investigators believe they had unusually large flocculi, brain lobes that link brain activity with body movement, and that their flocculi may have made this coordination more efficient than in modern birds and bats.

About 100 species are known, the earliest being dated in the Norian, about 225 Ma. They flourished worldwide during the Jurassic but were dying out by the late Cretaceous. See also **Azhdarchidae**. Late Triassic to end-Cretaceous, 225–66 Ma.

Pterygotidae a family of marine chelicerates in the order Eurypterida. They were generally large and had two pairs of eyes and a short, flattened telson ending in a short spine. They swam with their tail and two paddle-like appendages, for which they were named. The largest known is *Jaekelopterus*, estimated at 7–8 feet. Global distribution, Silurian to Late Devonian.

Pterygota the winged insects, a subclass of the class Insecta that includes almost all insects. (The pterygote insects are unrelated to the Pterygotidae (eurypterids) except as arthropods.) Traditionally divided into the infraclass Neoptera and the paraphyletic group Palaeoptera, the Pterygota are now reclassified in different ways which are still unsettled.

Pterygote referring to winged or secondarily apterous insects.

Pterygotid referring to the marine arthropods in the family Pterygotidae.

Pterygotus a genus of giant eurypterids in the family Pterygotidae. Growing as long as 6 feet, it is one of the better-known eurypterids. North and South America, Europe, and Australia; late Silurian to Middle Devonian.

Ptilodontoidea a superfamily of multituberculate mammals in the suborder Cimolodonta. Generally small and rodent-like, they are poorly known but probably derived from the Plagiaulacida. North America and Europe, Late Cretaceous to Eocene.

Ptilodus a North American multituberculate in the superfamily Ptilodontoidea and family Ptilodontidae. Squirrel-like and 1–2 feet long, it was widespread across North America, early to late Paleocene.

Ptychagnostus a genus of very small, blind agnostid trilobites in the family Ptychagnostidae. Less than half an inch long, it has two segments in the glabella and three in the pygidium. It was nektobenthic, generally living in the water column, and is found worldwide. *P. atavus* marks the beginning of the Drumian Age of the middle Cambrian at 504.5 Ma.

Ptychodus "layer tooth," a genus of early sharks in the extinct superfamily Hybodontoidea and family Ptychodontidae. About 30 feet long, *Ptychodus* is distinguished by its unusual dentition, which consisted of thousands of flat molar teeth, evidently used to crush bivalves and crustaceans. Cosmopolitan, Cretaceous to Paleocene.

Ptychoparia an early trilobite, the type genus of the order Ptychopariida. Like all in the family Ptychopariidae, its body narrows toward the small pygidium. Generally an inch long, it had small eyes with narrow, curving brow ridges and may have had long cephalic spines. North America and cosmopolitan, middle to late Cambrian.

Ptychopariida a large early order of trilobites that appeared, along with the Redlichiida and Corynexochida, early in the Cambrian. It is included in the proposed subclass Librostoma. The members of the order are diverse but generally had an oval shape and a small pygidium. Global distribution, early Cambrian to Late Ordovician.

Ptyctodontidae "folded teeth," a family of placoderm fish in the monotypic order Ptyctodontida, related to the Arthrodira and Phyllolepida. The ptyctodontids had large eyes, heads, and bodies and were weakly armored on head and shoulders. They are the only sexually dimorphic placoderms, the males having hooklike claspers on their pelvic fins. Now considered the most derived placoderms, they may be ancestral to the jawed vertebrates. Cosmopolitan, Middle to Late Devonian.

Ptyctolepis brachynotus a species of stem-sarcopterygian fish described in 2017. Possibly related to *Psarolepis*. China, Early Devonian.

Puertasaurus a genus of titanosaurian sauropodomorph dinosaurs closely related to *Argentinosaurus*. Known only from skeletal fragments of one individual, it is estimated to have been massive and as much as 130 feet long. Argentina, Late Cretaceous, 71–66 Ma.

Pugnax a genus of articulate rhynchonellid brachiopods in the family Pugnacidae. About 1 inch wide, it generally had a subtriangular shape and strong central ribs, often with a smooth shell. Global distribution, Devonian to Permian.

Puijila darwini a species of ancestral pinnipeds, the most primitive relative of the Phocidae, the earless seals. Known from one almost complete skeleton found in an Arctic lake-bed deposit, *Puijila* was otter-like and semiaquatic. It grew to 3 feet long and had a tail and four short legs with enlarged and possibly webbed feet. See also ***Enaliarctos*****.** Nunavut, Canada, late Oligocene to Miocene, 24–21 Ma.

"Pulmonata" the pulmonates, a large, polyphyletic group of snails and slugs that have lost their gills and breathe air by means of a kind of lung. Global distribution, Carboniferous to Recent.

Pulmonoscorpius kirktonensis a species of giant terrestrial scorpions more than 2 feet long; Scotland, Carboniferous, 320 Ma.

Punctate pierced by pores. In brachiopods, a condition in which elongated, regularly arranged cavities extend from the inside of the shell to the outside. Although all terebratulids are punctate and all atrypids and pentamerids are impunctate, the condition cuts across the other systematic boundaries.

Punctuated equilibrium an evolutionary model that sees most change as occurring in relatively brief bursts of evolutionary diversification, with longer periods of stasis in between. The idea is generally respected as an addition to the basic evolutionary principles of uniformitarianism and natural selection. See also **modern synthesis, phyletic gradualism**, **anagenesis**, and ***Metrarabdotos***.

Purgatorius a contentious genus of small mammals in the order Plesiadapiformes, possibly the last common ancestor of primates and plesiadapids. United States, Late Cretaceous? to early Paleocene.

Purpuroidea a genus of periwinkles, Mesozoic prosobranch gastropods in the superfamily Littorinoidea and family Purpurinidae, formerly classified in the discarded order Mesogastropoda. Characterized by a series of short, blunt spines on the top half and fine spiral ribs on the bottom, it had a thick, robust shell almost 3 inches high. Europe, Africa, Asia, and North America; Late Triassic to Early Cretaceous.

Pycnocrinus see ***Glyptocrinus*.**

Pycnodontiformes "flattened tooth," an order of laterally compressed actinopterygian fish. Flourishing in the Jurassic and Cretaceous, the pycnodonts were small- to medium-sized fish, characterized primarily by their almost circular shape and round and flattened teeth, which were designed to crush shellfish. See also ***Piranhamesodon***. Global distribution, Late Triassic to Eocene.

Pycnogonida the sea spiders, a class of marine arthropods usually placed in the subphylum Chelicerata. Not arachnids but closer to them than to other arthropods, they have small bodies and generally four pairs of long legs. Their size ranges from less than an inch to 3 feet. Cosmopolitan but especially large in the Antarctic, late Cambrian to Recent.

Pygasteridae Mesozoic sea urchins, a family of irregular euechinoids in the extinct order Pygasteroida. In the type genus *Pygaster*, the large periproct (the anal area) is keyhole-shaped. Europe, Middle Jurassic to Late Cretaceous.

Pygidium the tail segment of an arthropod, such as a trilobite.

Pygostyle the ploughshare-shaped element of fused bones at the base of the tail of modern birds.

Pyrotheria an order of large South American ungulates that includes two small families, the Pyrotheriidae and the Colombitheriidae. Sometimes called "false elephants," they had snouts a foot long and short, columnar limbs. Paleocene to Oligocene.

Q

Qingjiang biota an assemblage of early-Cambrian organisms described in 2019. Dated at 518 Ma, it is located about 500 miles north of the site of the possibly coeval Chengjiang biota. Its most abundant taxa are cnidarians and arthropods (including arachnids, crustaceans, insects, and millipedes). There are also basal chordates and possibly very significant organisms about 1.5 inches long that resemble the tiny enigmatic kinorhynchs found in modern substrates. Southern China, Hubei Province, early Cambrian.

Quadrijugatoridae a family of palaeocopid ostracods in the order Beyrichicopina and superfamily Hollinoidea; Canada, Late Ordovician.

Quadrops flexuosa an unusually spinose species of trilobites in the family Acastidae; synonym *Philonyx*. Between 3 and 6 inches long, *Quadrops* is characterized by curving spines around the entire body and especially by a four-pronged rostrum extending forward from the glabella. Morocco, Early Devonian.

Quagga a subspecies of South African plains zebras in the order Perissodactyla and genus *Equus*. The *Quagga* became extinct in the middle of the nineteenth century.

Quaternary extinctions the relatively abrupt extinctions of most of the large mammals in all continents during the middle and late Pleistocene. Most of these extinctions occurred after the arrival of hominins, although some researchers have pointed also to climate change or other factors as partial causes.

Quaternary Period the current division of geologic time, including essentially the Pleistocene Epoch and the current historical epoch, which is often referred to as the Holocene and dated from about 12,000 years before the present. The Quaternary is of course marked by the spread of modern hominins and by the extinction of many large terrestrial animals.

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Quercy caves an area where phosphate deposits in caves in southwestern France were mined up to the nineteenth century. The caves have produced a great number of mammal fossils dated between the Eocene and Pleistocene, although their dating is approximate.

Quetzalcoatlus a genus of large pterosaurs in the suborder Pterodactyloidea and family Azhdarchidae. With a very long neck and a sharp-pointed beak, *Quetzalcoatlus* had a wingspan of 40 feet; it closely resembles the Romanian discovery *Hatzegopteryx*. United States, Late Cretaceous, 68–66 Ma.

R

Radiation the evolutionary pattern of rapid appearance and dispersal of many diverse species of a lineage.

Radinskya an obscure genus of primitive perissodactyl mammals generally placed in the Laurasiatheria. Known only from a partial skull and jaw, it was the size of a small dog and is thought to be evidence of the radiation of the perissodactyls from Asia. China, late Paleocene.

Radiolaria a subclass of marine protists in the phylum Retaria, from 0.1 to 0.2 mm in diameter. Radiolarians are important stratigraphically in the absence of calcareous microfossils, but even their siliceous skeletons are dissolved by high concentrations of carbon dioxide in the ocean. Global distribution, Cambrian to Recent.

Radiolites a genus of rudistid bivalves in the order Hippuritida and family Radiolitidae. Up to a foot long, with valves that were unequal in size and shape, it was one of the unusual horn-shaped bivalves that were important reef-forming organisms in the Cretaceous. Europe, Asia, and North and South America; Early to Late Cretaceous.

Radiometric dating the technique of using the known rate of decay of radioactive isotopes to establish, within certain limits of certainty, the absolute age of strata of Earth's surface. The resulting dates are used with biostratigraphic information to establish the geologic time scale.

Radula a row of rasping chitinous teeth on a tongue-like structure behind the mandible of mollusks, a synapomorphy of the phylum.

Radulichnus an ichnogenus of trace fossils, the trace left on hard substrates by grazing limpets, other gastropods, chitons, and other radula-bearing grazers.

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Rafinesquina a genus of articulate brachiopods in the order Strophomenida and family Rafinesquinidae, very similar to ***Leptaena***, *q.v.* Global distribution, Ordovician to Silurian.

Ramapithecus see ***Sivapithecus*.**

Rangeomorphs a group of fern-shaped Ediacaran forms which may be an extinct stem group of organisms related to animals. Dated at 575–560 Ma, just before the Cambrian Explosion of multivariate animal forms, they may also be related to the even earlier sponges. At least two described species, *Rangea schneiderhoehoni* and *Fractofusus misrai*, are considered valid. Global occurrences, notably Russia, Canada, and Australia; Precambrian.

Raoellidae a still poorly known family of cetartiodactyl mammals in the clade Cetancodonta. The semi-aquatic *Indohyus*, the best-known genus, may represent a step in the transition of whale ancestors back to an aquatic environment. Southeast Asia, Eocene.

Rapetosaurus a monospecific genus of titanosaurian sauropod dinosaurs in the family Nemegtosauridae. *Rapetosaurus krausei* is known from an unusually complete skeleton of a juvenile and parts of three other individuals. Adults are estimated to have been up to about 50 feet long, much smaller than the largest titanosaurs. The juvenile is estimated to have grown fast, probably without any parental care, from about 8 pounds at hatching to about 90 pounds when it died about 2 months later, probably from starvation. Madagascar, Late Cretaceous, 70–66 Ma.

Raphidioptera an extant order of pterygote insects in the clade Neuropterida. Relatively primitive, the Raphidioptera are little changed since the Jurassic. They are especially identified by a long female ovipositor and by a narrowly elongate prothorax, which provides the common name snakeflies. Holarctic distribution, Jurassic to Recent.

Raphidonema a genus of calcareous sponges in the extant subclass Calcaronea and order Pharetronida. Cup-shaped and often twinned, *Raphidonema* forms large sponge beds in the Early Cretaceous of England. Europe and Asia, Cretaceous to Eocene.

Raphinae a subfamily of flightless birds in the family Columbidae. The family became extinct less than 300 years ago with the disappearance of the dodo (*Raphus cucullatus*) and the Rodrigues solitaire (*Pezophaps solitaria*) from the Mascarene Islands in the Western Indian Ocean. Mauritius and Rodrigues, Pleistocene to Recent.

Raphiophoridae a family of blind trilobites in the order Asaphida and superfamily Trinucleoidea. They are notable for very long, trailing genal spines and a single

spine extending forward from the triangular cephalon. The Raphiophoridae were the only family of Trinucleoidea to survive the Ordovician extinction. Global distribution, Early Ordovician to middle Silurian.

Raphus cucullatus the dodo, a flightless bird in the family Columbidae and subfamily Raphinae; also called *Didus ineptus* and *Struthio cucullatus*. About 3 feet tall, it was hunted to extinction by about 1800, as was its close relative *Pezophaps*. Mauritius, Pleistocene to Recent.

Raptorex kriegsteini a dubious species of dinosaurs known from a single fossil. It was once considered a possible ancestor of *Tyrannosaurus rex* but is now thought to be an unclassifiable juvenile specimen, possibly related to *Tarbosaurus*. China, Late Cretaceous.

Rastrites a short-lived genus of scandent graptolites in the order Graptoloidea. It was characterized by long, slender, isolated thecae standing out from a single linear stipe, each theca hooked at the tip. Global distribution, early Silurian.

Ratites large, flightless birds of the extant infraclass Palaeognathae. Mostly of Gondwanan origin, they include the modern rheas in South America, ostriches in Africa, emus in Australia, and probably the extinct moas of New Zealand. The name is derived from the Latin *ratis* (raft), chosen because ratites have a flat breastbone with no keel, and significant because the keel is crucial to anchoring wing muscles for flight. Although no fossils are known from the Cretaceous, genetic research indicates that the order probably originated before the end-Cretaceous extinction. The earliest-known ratites appeared in the Paleocene (see ***Diogenornis***). Several giant genera — such as *Dinornis*, *Aepyornis*, *Vorombe,* and *Dromornis* — became extinct after the arrival of humans in their habitats.

Rauisuchians an informal term for a group of crocodilian archosaurs of the Triassic, included in the clade Pseudosuchia. Up to 20 feet long, they were generally carnivorous and among the largest predators of the period. North and South America and Europe, Early to Late Triassic.

Ray-finned fishes see **Actinopterygii**.

Rayonnoceras a genus of pseudorthocerid nautiloids in the family Carbactinoceratidae. Orthoconic and generally about 3 feet long but up to 8 feet, they preyed on small sharks and other fish. Known from shallow-water environments in the United States and Europe, Early to Late Carboniferous.

Razanandrongobe a monospecific genus of sebecosuchian crocodylians described in 2017 as a mesoeucrocodylian and the earliest notosuchian. On the basis of several cranial fragments and large, serrated teeth, *R. sakalavae* is estimated to have been large enough to prey on large dinosaurs. Madagascar, Middle Jurassic, 170 Ma.

Receptaculitidae a family of benthic marine organisms, currently classified as calcareous algae. In the past it has been referred to the Porifera and is still controversial; see, *e.g.,* ***Ischadites***. Global distribution, late Cambrian to Early Triassic.

Red Gulch Dinosaur Tracksite a location in the Sundance Formation in northern Wyoming, displaying numerous footprints made by ceratosaurs walking on a beach of fine sand. United States, Middle Jurassic, 180–160 Ma.

Redlichia an early genus of trilobites in the order Redlichiida and family Redlichiidae. Ranging from 2 to 14 inches long, it had a semicircular cephalon, crescent-shaped eyes, a narrower thorax, and a small pygidium. In some species, such as *R. takooensis*, the large, crescent-shaped eyes gave it nearly 360-degree vision. Cosmopolitan, Cambrian, 516–501 Ma.

Redlichiida an early order of relatively flattened trilobites with a large cephalon, a many-segmented thorax, and a small pygidium. The Redlichiida appeared in the early Cambrian at about the same time as the Ptychopariida and Corynexochida, achieving global distribution but becoming extinct before the end of the Cambrian.

Remingtonocetidae a family of aquatic mammals in the suborder Archaeoceti, known mainly from ***Kutchicetus****, q.v.* Similar in appearance to amphibians like the crocodile, they had short limbs and a long, narrow skull with nostrils near the front. They could walk on land but were mainly aquatic. Pakistan and Egypt, early to middle Eocene.

Repenomamus robustus a species of eutriconodont mammals in the family Gobiconodontidae. About the size of an opossum or badger, it is especially notable for a Jehol specimen that contains the remains of a baby psittacosaur in its stomach, the first direct evidence that mammals were competing with dinosaurs for prey at the beginning of the Cretaceous. Bearing characteristics of reptiles as well as mammals, *Repenomamus* existed also as a much larger species, *R. giganticus*, which was 3 feet long and weighed more than 30 pounds. China, Early Cretaceous, 130 Ma.

Replacement the complete supplanting of minerals in a fossil by different minerals coming from the surrounding sediment, usually resulting in increased mass and hardness, and often preserving anatomical structure in detail. In exceptional circumstances, the organism may be replicated in three-dimensional detail, especially by pyrite, marcasite, calcium phosphate, kaolinite, or other relatively soft minerals. Under pressure and heat, aragonitic fossils (especially some mollusks and corals) often undergo recrystallization into calcite. See also **taphonomy**.

Reptilia a paraphyletic class of tetrapod amniotes that includes snakes, lizards, crocodiles, and turtles. Reptiles are distinguished by a tough, horny skin covered with scales, scutes, or plates, and those with limbs have claws on their toes. The class is technically defined as “nonavian, nonmammalian amniotes,” excluding

some descendants of tetrapods, namely, mammals and birds. The first reptiles evolved from amphibians in the Carboniferous as the colonization of the land by animals advanced, the earliest-known appearing in the Early Pennsylvanian (see ***Hylonomus*** and ***Paleothyris***). Global distribution, Late Carboniferous to Recent.

Reticulate or reticulated of animals' skin or fur, having pigment, veins, threads, fibers, or scales that create a netlike appearance.

Reticuloceratidae an important family of ammonoids in the order Goniatitida and superfamily Gastrioceratoidea. Several species of the genus *Reticuloceras* are index fossils in the Carboniferous**.** North America, Europe, and Asia; Late Carboniferous.

Revueltosaurus a genus of pseudosuchians originally considered an ornithischian dinosaur but now classified as a sister taxon of the aetosaurian suchians. Well-armored with a coat of bony plates and a tail club, it is known principally from several partial skeletons found in Arizona, at the *Revueltosaurus* Quarry in Petrified Forest National Park, and near Tucumcari, New Mexico. United States, Late Triassic, 230–205 Ma.

Rhabdinopora a genus of planktic colonial graptolites in the early order Dendroidea and family Anisograptidae. *Rhabdinopora* is thought to be the ancestor of the large order Graptoloidea. It is characterized by a conical reticulate colony with many parallel stipes that branch and bifurcate. The stipes are connected by dissepiments, forming a netlike surface and superficially resembling the bryozoan *Fenestella*. Global distribution, Early Ordovician.

Rhabdinopora flabelliformis "fan-shaped," a well-known species of graptolites long considered benthic and classified as *Dictyonema flabelliforme* but now known to be planktic. It is an important index fossil in determining the date of the Cambrian-Ordovician boundary. Europe, Early Ordovician.

Rhabdopleura an extant genus of small benthic colonial animals in the class Pterobranchia and family Rhabdopleuridae. It is a wormlike, sessile suspension feeder, probably related to the extinct graptolites. Global distribution, Cambrian to Recent.

Rhachiocephalus a genus of large dicynodont therapsids in the family Rhachiocephalidae or Cryptodontidae. From 6 to 8 feet long, it was one of the largest animals of its time. Tanzania and South Africa, late Permian, 259–254 Ma.

Rhachitomous a vertebral condition of some temnospondyl amphibians, traditionally used in their classification. Modern research has shown, however, that many early tetrapods have rhachitomous vertebrae, and that the condition is not a synapomorphy of any one group of temnospondyls.

Rhamphorhynchoids the basal pterosaurs that gave rise to the pterydactyloids in the Middle Jurassic. Previously considered a suborder, the group is paraphyletic, but the term is still used to refer in general to the early pterosaurs. Although all could fly, they were generally much smaller than the pterydactyloids, and they differed in having a long tail; also, most were well-toothed. The rhamphorhynchoids appeared about 230 Ma; among the earliest species are *Preondactylus*, *Peteinosaurus*, ***Dimorphodon*** (*q.v.*), and possibly the poorly known *Faxinalipterus.* The best known of the group is *Rhamphorhynchus*, which appeared later, about 151 Ma. Global distribution, Late Triassic (Norian) to Cretaceous.

Rhamphorhynchus a genus of fish-eating pterosaurs in the family Rhamphorhynchidae. *Rhamphorhynchus* was only slightly larger than a crow but had a wingspan of 4–5 feet and a very long tail, which ended in a characteristic diamond-shaped vane. Europe and Africa, Late Jurassic, 152–150 Ma.

Rhenanida an order of scaly marine placoderms. Flattened and raylike, they were bottom-dwelling predators, with armor consisting only of unfused tubercles and scales. Their fossil record is sparse but worldwide, Early to Middle Devonian.

Rhenops an unusual genus of phacopid trilobites in the large family Acastidae. *Rhenops* is characterized by stout genal spines, protruding eyes, and two dozen pairs of legs. Europe and South America, Middle to Late Devonian.

Rhenopyrgus a genus of small edrioasteroid echinoderms in the family Rhenopyrgidae. Its theca was turret-shaped, and its stem was composed of many plates; the total length was about an inch. Argentina, Morocco, France, and United States; Early Ordovician to Early Devonian.

Rhineuridae an extant family of burrowing squamate reptiles in the suborder Amphisbaenia. This family of wormlike lizards is found in Cenozoic strata across North America but is now known only as one genus in Florida. Middle Paleocene to Recent.

Rhinocerotidae an extant family of large perissodactyl mammals in the suborder Ceratomorpha and superfamily Rhinocerotoidea. This large family comprises about forty extinct genera as well as the modern rhinoceroses. Only late in their evolution did the latter group develop horns. North America, Europe, Asia, and Africa; Eocene to Recent.

Rhipidistia "fan sail," an extant subclass of lobe-finned bony fishes in the class Sarcopterygii. The name refers to large paired fins with bones, indicating a close relationship to tetrapods. The group includes numerous diverse extinct orders as well as the lungfishes, which are still represented by several genera. Global distribution, Early Devonian to Recent.

Rhizobiales "root life," an order of symbiotic bacteria, one of several groups that can produce the ammonium and nitrates used in fertilizers and gunpowder. These bacteria enable certain plant subfamilies of the order Fabales (principally the Papilionoideae and Mimosoideae) to fix atmospheric nitrogen in the form of ammonium and nitrates, eventually enriching the soil. In turn the bacteria benefit from flavonoids secreted by the plants. The rhizobia are known to have existed in the Precambrian, possibly for billions of years. Global distribution, Precambrian to Recent.

Rhizodontida an order of large predatory freshwater fish in the class Sarcopterygii. One species, *Rhizodus hibberti*, was at 23 feet long, probably the largest freshwater fish known. United States and Europe; Middle Devonian to Late Pennsylvanian.

Rhizome a rootlike plant stem that generally grows horizontally, on or beneath the ground surface.

Rhizomyinae an extant subfamily of myomorph rodents in the family Spalacidae, including the Asian bamboo rats and some African mole rats. Africa and Eurasia, Miocene to Recent.

Rhombifera a class (or subclass or order) of cystoid echinoderms, similar to the Diploporita and placed in either the Blastozoa or the Crinozoa. They are characterized by perforated plates in the calyx and rhombic thecal plates shared equally between adjacent plates. North America, Europe, and Asia; Early Ordovician to Late Devonian.

Rhombopora a genus of branching stenolaemate bryozoans in the order Rhabdomesida and family Rhomboporidae. The individual branches were sometimes spiny, with conspicuous openings in the skeleton wall through which the tentacles of the zooids extended for feeding. Global distribution, Ordovician to Permian.

Rhynchocephalia an extant order of lizard-like reptiles in the subclass Lepidosauria, a sister group to the Squamata. Rhynchocephalians were numerous in the Mesozoic but declined abruptly in the Paleogene. The order includes the large group of sphenodonts, which are now extant only in the tuatara (two species of *Sphenodon*) of New Zealand. Global distribution, Middle Triassic to Recent.

Rhynchocoelia see **Nemertea**.

Rhyncholepis a genus of early jawed fish in the order Anaspida. It is named "beaked scale" for its thick, bony scales. Scandinavia, late Silurian, 426–423 Ma.

Rhynchonella a large and long-lived genus of medium-sized brachiopods in the family Rhynchonellidae. Up to 2 inches in diameter, they are generally triangular and biconvex, with strong ribbing and a short hinge. Global distribution, Middle Ordovician to Eocene.

Rhynchonellata a very large class of articulate brachiopods in the subphylum Rhynchonelliformea. It includes the only living orders of articulate brachiopods, the Rhynchonellida, Terebratulida, and Thecideida. The extinct rhynchonellate orders are the Athyridida, Atrypida, Orthida, Pentamerida, Protorthida, Spiriferida, and Spiriferinida. Global distribution, early Cambrian to Recent.

Rhynchonellida an extant order of articulate brachiopods in the class Rhynchonellata. They were wedge-shaped, often resembling a nut, with astrophic hinges and no brachidia. Global distribution, Ordovician to Recent.

Rhynchonelliformea a subphylum of articulate brachiopods, replacing the class Articulata. Containing more than 4,500 genera, it is by far the largest of the 3 brachiopod subphyla. It comprises the extinct classes Chileata, Kutorginata, Obolellata, and Strophomenata, and the extant Rhynchonellata. In addition to articulation, the Rhynchonelliformea differ from the Linguliformea in having a fibrous secondary shell layer. Early Cambrian to Recent.

Rhynchosauria "beak lizard," an order of herbivorous diapsid reptiles, primitive archosauromorphs of the Triassic. The early rhynchosaurians were small and lizard-like, while some toward the end of the period grew to more than 6 feet long. These later genera had bulky bodies, a strong beak, and wide skulls, with some teeth becoming broad toothplates for cutting up plant material. Global distribution, Early to Late Triassic.

Rhynia a genus of early vascular land plants in the class Rhyniopsida. It is known only from the Rhynie chert, where it is a common rhizomatous plant with stems up to 8 inches high. Scotland, Early Devonian.

Rhynie chert a Lower Devonian Konservat-Lagerstatten that contains many early arthropod and plant fossils. It is especially important because it represents an early stage of the colonization of land by marine life and even the first evidence of herbivory by sap-sucking mites. A short turf a few inches high was created by early land plants, including bryophytes and the first vascular plants (see ***Rhynia*** and ***Trichopherophyton***), as well as pre-vascular plants with mixed bryophytic characteristics, such as *Aglaophyton* and *Horneophyton*. The informal term "rhyniophytes" is often used to refer to the Rhynie flora in general. The Rhynie fossils are mainly found in chert deposited around hot springs, and many are three-dimensional. Some of the significant animals are the earliest-known insect (***Rhyniognatha hirsti***), crustaceans (see ***Lepidocaris***), trigonotarbids, the oldest mites (see **Acari**), and harvestmen (see **Opiliones**). See also **Windyfield**. Scotland, 410–405 Ma.

Rhyniella praecursor a famous hexapodal arthropod of the Rhynie chert, placed in the order Collembola. Among the earliest-known proto-insects, it was 2 mm long and wingless. Scotland, Early Devonian.

Rhyniognatha hirsti the earliest-known insect, a species known from specimens found in the Rhynie chert, especially a dicondylic pair of mandibles. The presence of condyles and the short, triangular mandibles may indicate that *R. hirsti* had wings. Scotland, Early Devonian.

Rhyniopsida a class of primitive leafless plants in the division Tracheophyta. Among the simplest of all vascular plants, they bore sporangia near the tips of branches. First known from the Rhynie chert assemblage and now worldwide, Early Devonian.

Richthofenia an unusual genus of articulate strophomenate brachiopods in the order Productida and family Richthofeniidae. It is similar to cup-shaped rugose corals in shape and also in its reef-forming habit, with specializations for encrustation on hard substrates. United States, especially Texas, early Permian.

Ridersia a genus of echinoderms in the class Eocrinoidea. It had a high, slender cup, conical to almost cylindrical, from 3 to 4 inches long. Australia, late Cambrian.

Riojasaurus a genus of middle-sized early sauropod dinosaurs in the family Riojasauridae, probably related to the slightly smaller melanorosaurus of South Africa. Herbivorous and with a heavy body and massive legs, *Riojasaurus* was one of the very few sauropods in South America. About 33 feet long and weighing about 10 tons, it was mainly quadrupedal but optionally bipedal. Argentina, Late Triassic, 230–210 Ma.

Rissooidea an extant paraphyletic superfamily of very small marine and freshwater gastropod mollusks in the clade Littorinimorpha. Generally cylindrical or conical in shape, the group is extremely diverse and widespread. Global distribution, Jurassic to Recent.

Riversleigh a Cenozoic Konservat-Lagerstatten in northwestern Queensland that has produced exceptionally well-preserved specimens of bats, marsupials, insects, and other Australian fauna and flora. Many of the fossils are three-dimensional, having been preserved in soft, uncompressed limestone in surface and cave deposits. Australia, late Oligocene to late Miocene.

Robertia an early monospecific genus of herbivorous dicynodont therapsids in the family Pylaecephalidae, closely related to *Diictodon*. About a foot long, *R. broomiana* had two sharp canine teeth and a horny beak, probably used in digging. South Africa, middle to late Permian, 265–260 Ma.

Rock varnish a dark biogeochemical encrustation on exposed rock in almost any terrestrial weathering environment, but most commonly found as desert varnish in arid or semi-arid sites. Consisting primarily of iron and manganese oxides, clay, and carbonates secreted by bacteria, it is useful in identifying paleoenvironments.

Rodentia an order of gnawing mammals, with more than 4,600 species (more than 2,000 extant), the largest group of mammals. Ranging from 2 inches to several feet long (the capybara), they are characterized primarily by an upper and a lower pair of hypselodont, continuously growing incisors. Originating in Asia, according to some genetic estimates in the Late Cretaceous, they rapidly spread worldwide. The earliest specimens of rodents are from the Paleocene; see **Ischyromyidae** and **Paramyidae.** Exceptionally for placental mammals, rodents reached even Australia before the early Pliocene.

Rodhocetus kasrani a species of archaeocete whales in the family Protocetidae, an important recent discovery in strata deposited in deep water about 50 Ma, representing the earliest-known deep-ocean whale. It had paddle-like feet but is more notable for its unfused vertebrae that allowed it to swim principally with its tail as do modern whales. *Rodhocetus* still bore short but powerful hindlimbs and a pelvis connected to its sacrum. Similar to the slightly more recent *Protocetus* except that the latter could not have supported its own weight on land, whereas *Rodhocetus* may have been able to do so and therefore represents the farthest-known evolution of ancestral whales before they lost all useful terrestrial characteristics. It is also notable because its blowhole was high on its head, a step in the direction of modern whales, all of which have a blowhole on top of the head. Pakistan, early Eocene.

Rodinia "Motherland," a Russian name given to a Proterozoic supercontinent that existed between 1300 and 650 Ma. It consisted of fragments from an earlier supercontinent called Columbia or Nuna that had drifted apart between 1800 and 1500 Ma. Rodinia centered on Laurentia (which was on the Equator) and seems to have been essentially barren of life except for single-celled algae.

Rodrigues solitaire see ***Pezophaps*.**

Romer's gap the paucity of tetrapod and arthropod fossils in the period between 361 and 340 Ma at the beginning of the Carboniferous period, also called the Tournaisian Gap. The first terrestrial vertebrates appeared at the end of the Devonian, around 370 Ma, but their fossil record in the early Mississippian is very thin. (See also **Tetrapoda** and ***Tulerpeton*.)** Terrestrial vertebrates appear in great numbers in the Middle Mississippian, so their radiation at the beginning of the period must have been quite rapid.

Rosamygale grauvogeli a species of funnel spiders in the infraorder Mygalomorphae and extant family Hexathelidae. Less than half an inch long, *R. grauvogeli* is the earliest-known mygalomorph spider. Known only from the Grès à Voltzia, France, Early Triassic.

Rostroconchia a class of mollusks superficially similar to bivalves and once proposed as ancestral to them. Both, however, along with the brachiopods, appeared close to the same time in the Cambrian Explosion near the beginning of the Paleozoic Era, and their interrelationships remain unclear. From 1 to 6 inches wide, the rostroconchs had a taco-like shell and a rostrum, a tube extending outside the shell, possibly to filter the water. They diversified rapidly worldwide through the Ordovician, then declined in comparison to the bivalves, and became extinct at the end of the Permian.

Rotalipora globotruncanoides a species of planktic foraminiferans whose first appearance marks the beginning of the Late Cretaceous at 100.5 Ma; France.

Royal Tyrrell Museum a large paleontology museum in Drumheller, Alberta, devoted mainly to specimens from western Canada, especially from Dinosaur Provincial Park.

Rubeosaurus a genus of ceratopsian dinosaurs in the subfamily Centrosaurinae. Named "thornbush" for its array of horns and spikes, it had a single short horn on its snout and longer horns on its neck frill. Known from two specimens of skull fragments, it is estimated at about 19 feet and 2 tons. North America, Late Cretaceous, 75 Ma.

Rubidgea a monospecific genus of therapsids in the family Gorgonopsidae. *R. atrox* is notable for canine teeth longer than those of *Tyrannosaurus rex*; known principally from two skulls, it is estimated at 9–11 feet long. South Africa, late Permian, 259–254 Ma.

Rudists see **Hippuritida.**

Rugops primus a species of ceratosaurian theropod dinosaurs in the family Abelisauridae. Known only from a single skull, it is estimated at 15–20 feet long and thought to be carnivorous but probably a scavenger. Niger, Late Cretaceous, 96–94 Ma.

Rugosa the "wrinkled" corals, a large order of anthozoan cnidarians in the subclass Hexacorallia, synonym Tetracorallia. The Rugosa and the Tabulata were the most diverse and widespread coral reef-builders of the Paleozoic. Mainly conical or horn-shaped, they were generally solitary but sometimes colonial. The rugose corals

were generally composed of calcite, as opposed to the more easily dissolved aragonite of the modern Scleractinia. The first undoubted Rugosa appeared in the Middle Ordovician and became dominant in the middle Silurian as the Tabulata declined. The Rugosa became extinct at the end of the Permian.

Rugosodon eurasiaticus a species of multituberculate mammaliaforms in the order Paulchoffatiidae. Found in the Tiaojishan Formation and dated at about 160 Ma, *Rugosodon* is so called because of its distinctively wrinkled teeth. It was omnivorous, and its chipmunk-sized body was 6–7 inches long and adapted to tree-dwelling. Yanliao biota, China, Late Jurassic.

Rukwapithecus fleaglei name tentatively given to a genus of apes in the superfamily Hominoidea. Possibly the earliest-known catarrhine at 25 Ma, it is known only from a jaw fragment and four teeth. See also ***Kamoyapithecus*.** Tanzania, late Oligocene.

Ruminantia a suborder of artiodactyl ungulates that have a four-part stomach to digest tough plant material. The Ruminantia include cattle, sheep, goats, antelopes, deer, pronghorns, giraffes, and many extinct pecorans. Certain other ungulates with a slightly different digestive system — such as the tylopods (the camelids) and macropods (kangaroos and wallabies) — are considered "pseudo-ruminants." Global distribution, early Eocene to Recent.

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Sacabambaspis a genus of early pteraspidomorph craniates in the order Arandaspidiformes, closely related to *Arandaspis* and among the earliest whole-body specimens of ostracoderms. Jawless and 10 inches long, *Sacabambaspis* had a laterally flattened body covered with scales, and its extended tail ended in a small fin web; it had no paired fins. Its blunt head was armored with bony plates, with forward-facing eyes. First found in Bolivia, it is known from several Gondwanan locations: Argentina, Australia, and the Arabian Peninsula; Middle to Late Ordovician, 470–453 Ma.

Saccocoma a genus of stemless crinoids in the order Cladida and family Saccocomidae. Well-known from the Solnhofen quarry, it was very small with long, coiling arms. It has long been considered pelagic, but some research indicates that it may have been benthic. Europe, North Africa, and possibly Cuba; Early Triassic to late Cretaceous.

Saccoglossus an extant genus of acorn worms, enteropneusts in the family Harrimaniidae. The most speciose genus in the family, its fossils are known mainly from the Mazon Creek site; Early to Middle Pennsylvanian.

Saccorhytus coronarius the earliest-known species of deuterostomes, tentatively placed in the subphylum Vetulicolia; it was described in 2017 from a group of 45 individuals. Only 1 mm long, its globular body seems to have only one opening, which is surrounded by conical protuberances. China, early Cambrian, 540 Ma.

Sacculina a genus of parasitic barnacles in the order Cirripedia and family Sacculinidae. *Sacculina* is a small, shell-less, saclike animal that parasitizes crabs by attaching itself underneath and penetrating the crab's body with long, branching filaments that feed the parasite. Since it has no hard parts, it has not yet appeared in

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the fossil record. Its host, the green crab *Carcinus maenas*, however, is known from North America since the Eocene, and *Sacculina* may have appeared at some later time.

Saddle an anterior-pointing fold in the suture line of an ammonoid.

Sagenocrinites a genus of crinoids in the order Sagenocrinida. It is characterized by an ovoid crown and a conical cup half the height of the crown and about an inch in diameter, with branching arms well differentiated from the calyx. North America and Europe, Silurian.

Sagenopteris see **Caytoniales.**

Saghatherium a genus of primitive hyracoid mammals in the extinct family Pliohyracidae and subfamily Saghatheriinae. It was scansorial and herbivorous and was similar in some features to the modern hyraxes of the Procaviidae. Fayum, Egypt, late Eocene or early Oligocene.

Saharagalago a genus of bush babies, lorisid primates in the suborder Strepsirrhini and family Galagidae. Dated between 40 and 37 Ma, the early bush babies *Saharagalago* and a cousin *Karanisia* were discovered around 2000, pushing back the date of the earliest lorisiforms by 20 million years. They represent the earliest-known examples of the characteristic strepsirrhine toothcomb. Fayum, Egypt, middle Eocene.

Sahelanthropus tchadensis a species of hominids found near Lake Chad in 2001. This early hominid lies near the divergence of humans from chimpanzees, although probably predating it slightly. It shows a mix of human and chimpanzee characters and at 6.9 million years old is the earliest-known hominid.

St. George Dinosaur Discovery Site an in-place trackway of exceptionally well-preserved Early Jurassic dinosaur tracks now enclosed in a museum on the Johnson Farm in southwestern Utah.

Salientia "jumpers," the clade that includes the modern frogs, Anura, and their most closely related ancestors.

Saltasaurus loricatus a species of titanosaurian sauropod dinosaurs in the monospecific family Saltasauridae. About 40 feet long and weighing 8 tons, it was unusual for a sauropod in having osteoderms and armor plates covering its upper body and sides. Argentina, Late Cretaceous, 71–69 Ma.

Salterella an enigmatic small, conical fossil, widespread in North America in the Cambrian. Its stratified walls are composed of agglutinated grains of calcite. It superficially resembles some early cephalopods but is now tentatively referred to

the proposed phylum Agmata. North and South America and Europe, early Cambrian to Late Ordovician.

Saltoposuchus connectens the type species of a genus of relatively small, bipedal sphenosuchian reptiles in the superorder Crocodylomorpha. It was 3–5 feet long and weighed 30–35 pounds. Europe, Middle Triassic.

Saltopus elginensis "leaping foot," a genus of early dinosauriform reptiles, placed by some in the family Silesauridae. It is poorly known, mainly from casts of a partial skeleton. It has been studied intensively since its discovery in 1910 and classified variously as a stem dinosaur or a dinosauriform outside the clade Dinosauria. A reclassification proposal in 2017 considers it simply as a possible ancestor of the dinosaurs. Scotland, Late Triassic, 228 Ma.

Samotherium a genus of artiodactyl mammals in the family Giraffidae. It is similar in appearance to the modern okapi but with two long ossicones extending upward from the skull. Intermediate in size between the okapi and the modern giraffe, *Samotherium* seems to be a transitional form between early and modern giraffes. Although it may be related to *Palaeotragus* and *Giraffokeryx*, its ancestry is still undetermined. Europe, Asia, and Africa; Miocene to Pliocene.

Sanmiguelia lewisii a species of early plants that may belong to a stem group of angiosperms, known from several localities in western North America. One especially well-preserved autochthonous specimen was found in a Late Triassic streamside paleosol near Palo Duro Canyon in northwest Texas. Buried in its growth position, it is notable for several structures similar to angiosperms. United States, Late Triassic to Early Jurassic.

Sampling the collection and study of fossil specimens, varying according to many factors, especially the preservability of the taxon.

Sand dollar see **Echinoidea**.

Saniwa ensidens a species of monitor lizards in the family Varanidae, closely related to the genus *Varanus*. *S. ensidens* was 4–7 feet long, two-thirds of its length being its tail.

It is especially notable for two eyelike photosensory organs at the top of the head, called the pineal and parapineal organs, which are known today only in the lamprey. Although many reptiles and some vertebrates have similar structures, the function of these organs is unclear. It is known definitively only from Wyoming, but other species of *Saniwa* from Europe have been proposed. United States, early Eocene.

Santa Maria Formation a rock formation in Southern Brazil with strata dating from the Ladinian to Carnian ages, similar to those of the Chañares Formation of Northwestern Argentina. It is notable for specimens of early dinosaurs, aetosaurs, and cynodonts. Brazil, Middle to Late Triassic.

Santana Formation a Lower Cretaceous Konzentrat-Lagerstätte in the Araripe Basin of Northern Brazil. It is dated uncertainly between 112 and 106 Ma, slightly later than the neighboring Crato Formation. The Santana fossils, occurring inside limestone concretions, include complete specimens of fish in great numbers; partial specimens of pterosaurs with soft-tissue preservation of webbing; dinosaurs, including spinosaurids and coelurosaurs; reptiles (see **Araripesuchus)**; and a few insects and other invertebrates. Brazil, Early Cretaceous.

Sarcopterygii "flesh fin," lobe-finned fish in the superclass Osteichthyes. Previously called Crossopterygii, the Sarcopterygii appeared in the late Silurian along with other osteichthyans. They dwindled during the Mesozoic, eclipsed by the many very successful actinopterygians. The Sarcopterygii are still represented by several genera, including the coelacanths in the subclass Actinistia and the lungfishes in the subclass Rhipidistia. Among the many extinct sarcopterygian taxa, the closely related tetrapod lobe-fins of the Late Devonian are especially significant evolutionarily as the first terrestrial vertebrates. See also **Actinopterygii** and **Tetrapoda**.

Sarcosuchus imperator a very large crocodyliform reptile in the family Pholidosauridae, first discovered in 1964 in the Ténéré Desert of Niger. From 37 to 40 feet long, with a head more than 5 feet long and jaws about 4 feet long, it weighed around 9 tons, about 1.5 times as much as an African elephant. *Sarcosuchus* had a bulbous protuberance on the end of its snout, probably used to locate prey by smell or sound. North Africa and South America, Early to Late Cretaceous.

Sarkastodon mongoliensis a species of large mammals, hyperpredators in the family Oxyaenidae. Known only from a skull and jawbones with robust, hyena-like teeth, *Sarkastodon* is estimated at 10 feet long and almost 1 ton. Mongolia, late Eocene, 36–35 Ma.

Sarmientosaurus musacchioi a species of titanosaurian sauropod dinosaurs found in Patagonia and described in 2016. Estimated at about 40 feet long and 10 tons, it is known from an almost complete skull and several articulated vertebrae that may indicate a drooping posture of the head. It is also distinguished by its very large eyes. Argentina, Late Cretaceous, about 95 Ma.

Sasayamamylos a monospecific genus of basal eutherian mammals in the order Asioryctidae. Insectivorous, known only from a skull found in Japan in 2007 and described in 2013, *S. kawaii* may be the earliest-known example of a modern mammalian dentition. Early Cretaceous, 112 Ma.

Saturnalia tupiniquim a species of basal sauropodomorph dinosaurs, placed tentatively in the family Guaibasauridae. Although poorly known, *Saturnalia* is one of the earliest dinosaurs. Known mainly from partial skull and skeletal specimens found in Brazil, *Saturnalia* was 4–5 feet long and may have been omnivorous. A

partial femur from Zimbabwe has also been identified with the genus. Brazil and Zimbabwe, Late Triassic, 233 Ma.

Saurichthyidae a speciose family of Mesozoic ray-finned chondrostean fish in the order Saurichthyiformes. They were about 3 feet long and very slender, with symmetrical dorsal and anal fins near the tail, a shape that probably made them fast and efficient predators. They may have originated toward the end of the Permian but were common throughout the Triassic and persisted at least to the Middle Jurassic (see ***Saurorhynchus***). North America, Europe, Asia, Australia, and Madagascar; Early Triassic to Middle Jurassic.

Saurischia one of the basic divisions of dinosaurs, characterized especially by a three-pronged pelvic structure similar to that of most reptiles, with a pubis bone pointing downward and slightly forward. The earliest saurischians (such as *Eoraptor* and the Guaibasauridae) appeared during the Carnian Age of the Late Triassic. The sauropods are the most prominent group within the Saurischia, while the theropods are variously considered as saurischians or part of some other division (see **Ornithoscelida**). Global distribution, Triassic to Late Cretaceous, 233–66 Ma.

Saurolophus "lizard crest," a genus of large hadrosaurid dinosaurs in the subfamily Saurolophinae. From 30 to 40 feet long, they had a "duckbill" and a backward-extending cranial crest of unknown function. See also ***Parasaurolophus***. North America and Asia, Late Cretaceous, 71–68 Ma.

Saurophaganax a genus of very large theropod dinosaurs in the family Allosauridae. Variously estimated between 34 and 43 feet long, it is known only from fragmentary remains, mainly from Oklahoma. United States, Late Jurassic, 156–146 Ma.

Sauropoda an infraorder of quadrupedal sauropodomorph dinosaurs. Semiaquatic and herbivorous, the sauropods had very long necks, long tails, and a heavy body supported by four pillar-like legs. Estimates of sauropod weight vary greatly, but they were clearly the largest terrestrial animals known, with estimates ranging from 50 to 100 tons for the largest. Global distribution, Late Triassic to Late Cretaceous, 210–66 Ma.

Sauropodomorpha a clade of herbivorous saurischian dinosaurs that includes the infraorders Plateosauria and Sauropoda and their immediate ancestors. Early sauropodomorphs were bipedal and omnivorous; as succeeding species became herbivorous and heavier, they became quadrupedal, and the hindlimbs were shorter than the forelimbs in later groups. With representatives dated between 233 and 66 Ma (see ***Saturnalia***), the sauropodomorphs were the dominant terrestrial herbivores worldwide from the Late Triassic to the Late Cretaceous.

Sauroposeidon a genus of titanosaurian sauropod dinosaurs. At about 60 feet high, it was possibly the tallest dinosaur, and it had a longer neck than any other dinosaur,

conservatively estimated as 40 feet long, with some vertebrae 5 feet long. Estimated at 110 feet long and 60 tons, *Sauroposeidon* was significantly larger than its cousin *Brachiosaurus* but smaller than others such as *Argentinosaurus*. United States, Early Cretaceous, about 110 Ma.

Sauropsida a large group of advanced amniotes in the clade Reptiliomorpha, including dinosaurs, pterosaurs, birds, and all modern reptiles. The Sauropsida split off from the other main group of advanced amniotes, the Synapsida, in the Late Carboniferous, about 320 Ma. About 90 million years later, the first dinosaurs evolved from a sauropsid ancestor.

Sauropterygia a superorder of aquatic diapsid reptiles characterized especially by pectoral and pelvic girdle adaptations that supported strong flippers. Including the nothosaurs, plesiosaurs, and pliosaurs, the sauropterygians arose at the beginning of the Triassic from terrestrial ancestors; one of the earliest groups is the Pachypleurosauria. They diversified worldwide, with the plesiosaurs surviving into the Jurassic and the pliosaurs appearing in the Early Jurassic. The last of the sauropterygians disappeared at the end of the Cretaceous, except that some research now indicates that modern turtles may be distant descendants. Early Triassic to Late Cretaceous.

Saurorhynchus a genus of chondrostean fish in the order Saurichthyiformes and family Saurichthyidae; formerly called *Acidorhynchus*. Gar-like in appearance, it was 2–3 feet long and slender, with symmetrical dorsal and anal fins near the tail. Canada and Europe, Early to Middle Jurassic.

Savanna term used to refer to a wide range of environments between dense forest and desert, usually referring to openly wooded grassland.

Savannasaurus elliottorum a species of titanosaurian sauropod dinosaurs described in 2016. *Savannasaurus* was 50 feet long and is the most complete specimen of a sauropod found in Australia. Late Cretaceous, 100–94 Ma.

Scandent of vines and graptolites: having a climbing habit.

Scandentia an order of euarchontan mammals, now represented by two families in Southeast Asia, the Tupaiidae and the Ptilocercidae. Considered transitional between primates and their insectivorous ancestors, they are called tree shrews because of body similarities but are not shrews and are only partly arboreal. The earliest genus is *Eodendrogale*, a middle Eocene specimen poorly known from only a few teeth found in China. Asia, Eocene to Recent.

Scansorial of animals: able to climb trees, spending at least part of the time in an arboreal environment.

Scansoriopterygidae a family of small theropod dinosaurs known only from two partial skeletons. It is a significant group for having both feathers and a bat-like wing membrane. Found in 2015 and 2019, respectively, *Yi Qi* and *Ambopteryx longibrachium* were only about a foot long. China, Late Jurassic, 165–160 Ma.

Scansoriopteryx see ***Epidendrosaurus***.

Scaphites a genus of small, loosely coiled ammonoids in the order Ammonitida and suborder Ancyloceratina. Probably a slow swimmer, mainly benthic, it is named for a striking boat-shaped shell 2–5 inches long, with an involute and compressed juvenile stage, then a straight segment in the middle, and an erect terminal stage bending back over the juvenile stage like a hook. Several species are index fossils in the Late Cretaceous. Global distribution, 105–70 Ma.

Scaphopoda "boat foot," an extant class of infaunal marine mollusks, probably the latest class of mollusks to appear. Called "tusk shells," they are characterized by a tooth-shaped, curving, tapering shell, open at both ends. From 1 to 4 inches long, they live in the soft substrate offshore, beyond the intertidal zone, the only mollusk known to do so. The two orders are the Gadilida (the smaller species) and the better-known Dentaliida (the larger species). By far the most prominent genus is ***Dentalium***, *q.v*. Global distribution, Ordovician to Recent.

Scelidosaurus a genus of basal ornithischian dinosaurs, considered a thyreophoran and possibly related to *Scutellosaurus*. Quadrupedal, about 13 feet long, and protected by osteoderms along its neck, back, and tail, the herbivorous *Scelidosaurus* may be the earliest basal ankylosaur. England, Ireland, and China; early Jurassic, 197–183 Ma.

Scenella an enigmatic genus of early-Paleozoic limpet-like vertebrates, variously considered a monoplacophoran, gastropod mollusk, helcionellid, and even hydrozoan. About half an inch across, it had a high, curving, cap-shaped shell with radial and concentric striations. Global distribution, Cambrian to Ordovician.

Schizaster a genus of atelostomate heart urchins in the order Spatangoida and family Schizasteridae. Its ancestor ***Linthia*** appeared in the Cenomanian (94 Ma) and was prominent in the Eocene and Miocene. The evolutionary changes that resulted in ***Schizaster*** seem to be adaptations to living in finer-grained substrates. Global distribution, early Paleocene to Recent.

Schizasteridae a family of atelostomate heart urchins, irregular euechinoids in the order Spatangoida and suborder Paleopneustina. Global distribution, Late Cretaceous (94 Ma) to Recent.

Schizochroal a type of compound eye found only in some phacopid trilobites. Schizochroal eyes have up to 700 lenses with separate corneas, with larger lenses than in the holochroal eyes of most trilobites.

Schizoneura a genus of small, slight sphenophyte trees in the order Equisetales, related to the Calamitaceae; global distribution, early Permian to Late Jurassic.

Schloenbachiidae a family of ammonoids in the order Ammonitida and superfamily Hoplitoidea. With a complex ammonitid suture and a compressed form, they were irregular, some genera smooth and involute and others strongly ribbed and evolute. Europe, Asia, and Mexico; Cretaceous, 113–94 Ma.

Schubertellidae a family of foraminiferans in the superfamily Fusulinoidea. They diversified greatly toward the end of the Permian but became extinct at the end of the period. North America, Europe, and Asia; Pennsylvanian to late Permian.

Schuchertella a speciose genus of strophomenate brachiopods in the order Orthotetida. With both valves flat or gently curved, it had fine ribs and a wide, strophic hinge line. Global distribution, Late Ordovician to late Permian.

Schwagerinidae a family of large, complex foraminiferans in the superfamily Fusulinoidea. The genus *Schwagerina* is important in petroleum geology, providing several index fossils in Lower Permian strata. North and South America, Europe, and Asia; Late Carboniferous to late Permian.

Scincomorpha an extant clade of lacertilian squamates, generally considered paraphyletic. Its makeup is disputed, but the principal family (Scincidae, the skinks) is one of the largest and most diverse groups of lizards. Global distribution, Cretaceous to Recent.

Sciuridae the extant family of rodents that includes modern squirrels, little changed since the Miocene. Global distribution, Oligocene to Recent.

Sciurumimus albersdoerferi a species of coelurosaurian theropod dinosaurs placed tentatively in the superfamily Megalosauroidea. Reported in 2012 and known only from a juvenile specimen 28 inches long, it is named "squirrel mimic" for its tail feathers resembling a squirrel's tail fur. Germany, Late Jurassic, 150 Ma.

Scleractinia "hard-rayed," an extant order of anthozoan cnidarians, corals placed in the subclass Hexacorallia but with obscure origins. Often called stony corals, they are mostly colonial in relatively shallow water, with some solitary genera found in deeper water, some even abyssal. When the mainly calcitic tabulate and rugose corals disappeared at the end of the Permian, there were no important reef-building animals until the aragonitic scleractinians appeared in the Middle Triassic, sometime before 240 Ma. They seem to be unrelated to the earlier corals, but their evolutionary history is unknown.

The scleractinians became dominant reef-builders late in the Triassic. They are almost all aragonitic; only one purely calcitic genus, *Coelosmilia*, is known. They diversified in the Jurassic and spread globally in the Cretaceous. Many groups became extinct in the end-Cretaceous extinction, leaving the Mussinae, Faviinae, and Caryophylliidae as the principal modern survivors. Middle Triassic to Recent.

Scolecodonts the chitinous jaws of marine polychaete annelid worms. As large as a few millimeters, scolecodonts appeared in the Cambrian, were common in Ordovician and middle Paleozoic strata, became rare at the end of the Permian, recovered in the Mesozoic, and again became rare at the end of the Cretaceous. At least seven families of modern polychaetes have chitinous teeth that would be considered scolecodonts if fossilized. Cambrian to Recent.

Scolosaurus a monospecific genus of armored ornithischian dinosaurs in the subfamily Ankylosaurinae. Called "horned toad dinosaur" for the many spines of various sizes that protrude from its head, body, and tail, *S. cutleri* grew as long as 20 feet and weighed 2 tons. It is the earliest-known North American ankylosaur, known only from a single skeleton dated at about 76.5 Ma. Alberta, Late Cretaceous.

Scorpiones an extant order of chelicerates in the class Arachnida. Different from eurypterids but possibly related to them, scorpions appeared in the middle Silurian, around 430 Ma. They are elongated, with a segmented, curved tail tipped with a venomous stinger; the jaw has two chelicerae, larger in the earliest than in those of the late Paleozoic. They have eight walking legs and two pincer-like pedipalps, which are much longer in the earlier species. Their early fossil record is very sparse, but the oldest scorpions were probably aquatic or amphibious; by the Late Devonian, they seem to be completely terrestrial. The earliest are known from only partial appendages; see ***Brontoscorpio***, ***Gondwanascorpio***, and ***Proscorpius***. Global distribution, middle Silurian to Recent.

Scrotifera a proposed clade of placental mammals, based on molecular phylogenetic research, generally taken to include the orders Artiodactyla, Carnivora, Cetacea, Chiroptera, Perissodactyla, and Pholidota. As the name indicates, almost all scrotiferans carry their testes in a scrotum, but it is not a defining characteristic since several other placental groups also do so.

Scute an external ossicle, a plate of bone embedded in the skin, sometimes covered with horn, common in many dinosaurs and some mammals.

Scutellosaurus a genus of basal ornithischian dinosaurs. Considered a thyreophoran and possibly related to *Scelidosaurus*, *Scutellosaurus* was herbivorous and basically bipedal, differing greatly from later thyreophorans. About 4 feet long and weighing about 20 pounds, it was armored by several rows of small osteoderms from neck to tail. Northern Arizona, United States, Early Jurassic.

Scutosaurus a genus of large early reptiles in the family Pareiasauridae, the largest herbivore of the late Permian. From 8 to 10 feet long, it was heavily armored with scutes, osteoderms, and small skull spikes. Unlike most other pareiasaurs, *Scutosaurus* had its legs directly under its body. Russia, late Permian.

Scyphocrinites a genus of large crinoids in the order Monobathrida and family Scyphocrinidae. Sometimes found massed, it had a calyx up to 6 inches long, many branching arms, and a slender stem; it is considered pelagic; and some researchers think it hung down from a bulbous flotation device. Global distribution, late Silurian to Early Devonian, 416–412 Ma.

Scyphozoa the jellyfish, a class of cnidarians. They probably date back to the Precambrian, but fossils are rare because of the lack of hard parts. One of the earliest well-identified is *Essexella*, 3–4 inches wide, which is known from many specimens in the Mazon Creek fauna of the Late Carboniferous.

Sea lily common name for pelmatozoan crinoids, which are attached to the substrate by a stalk.

Sea pen see **Pennatulacea**.

Sea squirt see **Tunicata**.

Sea urchin see **Echinoidea.**

Sectorial tooth a single-cusped, pointed tooth, known especially in nonhuman primates, often with a cutting edge capable of a scissor-like action in occlusion.

Seed fern see **Pteridospermatophyta**.

Segnosaurus a genus of herbivorous theropod dinosaurs in the family Therizinosauridae. From 18 to 20 feet long and weighing a little more than a ton, it is characterized by very long, broad, flattened claws on the large forelimbs, strong hindlimbs, and cutting denticles on the edges of peg-like teeth. Asia, Late Cretaceous, 90 Ma.

Seirocrinus subangularis a species of large isocrinid crinoids in the family Pentacrinitidae. With a stem several feet long and a feathery calyx as much as 3 feet wide, it is often found attached to pieces of wood. Complete specimens are well-known from the *Posidonia* Shale of Germany, and it is also found in Canada and Alaska. North America and Europe, Early Jurassic, between 200 and 183 Ma.

Seismosaurus see ***Diplodocus*.**

Seitaad a monospecific genus of sauropodomorph dinosaurs found in Southern Utah in 2004 and described in 2010, probably an early sauropod. *S. ruessi*, known only from a headless but articulated skeleton, was 10–25 feet long and was probably herbivorous. United States, Early Jurassic, 185 Ma.

Selachii the sharks, a superorder of chondrichthyan fish in the subclass Elasmobranchii. The only Paleozoic elasmobranchs, the first sharks appeared about 420 Ma and diversified rapidly, becoming the dominant marine predators in the Devonian. The best-known early shark is the North American *Cladoselache*, and another early genus similar in appearance to modern sharks is *Denaea*, of the Carboniferous. Two with very unusual characters were ***Stethacanthus*** and ***Falcatus***, *q.v.* The selachians declined in the Carboniferous and Permian but rebounded in the Jurassic. Most modern sharks have their roots in the Cretaceous and diversified widely in the Cenozoic, as did most other modern elasmobranchs. Global distribution, late Silurian to Recent.

Selaginella an extant genus of spikemosses in the division Lycopodiophyta and class Isoetopsida. It is related to the giant club mosses of the Mesozoic. Global distribution, Silurian to Recent.

Selenodont dentition "crescent tooth," low-crowned teeth with a hard chewing surface and cusps forming a crescent shape when viewed from above; common in ruminant mammals.

Selenopeltis an Ordovician genus of trilobites in the order Odontopleurida and family Odontopleuridae. From 4 to 6 inches long, it is distinguished by many long pleural spines and a rectangular carapace. Europe and North Africa, Early to Late Ordovician.

Selkirkia a genus of predatory priapulid worms in the family Selkirkiidae, known primarily from the Burgess Shale. About 3 inches long, it lived in a tube, oriented vertically in the sediment, extending its proboscis to capture prey. North America (possibly also South America and Antarctica), middle Cambrian.

Semionotidae a family of non-teleost neopterygian fish in the order Semionotiformes. Widespread in the Mesozoic but extinct at the end of the Cretaceous. Global distribution, late Permian to Late Cretaceous.

Semionotus a genus of early neopterygian fish in the order Semionotiformes, the type genus of the family Semionotidae. Only 5 inches long, its habitat was mainly freshwater, but *Semionotus* is also found in marine deposits. It is notable for its peg-like teeth and an almost-square dorsal fin pointing backward. Cosmopolitan, Middle Triassic to Early Cretaceous.

Septum plural septa; a transverse partition inside the skeleton of an animal, especially in corallites, foraminiferans, and the shells of ammonoids, belemnites, and nautiloids.

Sequoia jeholensis a species of coniferous trees in the order Pinales and family Cupressaceae. Known especially from the Jehol Biota, it was widespread in the Holarctic in the Cretaceous. North America, Europe, and Asia; Jurassic to Oligocene.

Serpentes a suborder of squamate reptiles in the clade Ophidia, generally referring to modern snakes.

Serpula name given to several obscure types of worm tubes that are possibly related to the modern family Serpulidae; Silurian to Recent.

Serridentinus see ***Gomphotherium***.

Sessile stationary on the bottom sediment and often anchored directly to the substrate.

Setae slender, rigid, bristle-like extensions on living organisms. The term usually refers to bristles or hairs on animals, usually to arthropods. See also **chaetae**.

Sexual dimorphism see **dimorphic**.

Seymouria a genus of semiaquatic stem amniotes in the family Seymouriidae. It was 2–3 feet long and had several reptilian adaptations. Closely related to ***Discosauriscus***, *q.v.*, *Seymouria* is known primarily from the Texas Red Beds. United States and Germany, early Permian, 280–270 Ma.

Seymouriamorpha an order of reptile-like stem-tetrapods, generally placed in the clade Batrachosauria. North America, Europe, and Asia; early to late Permian.

Shansisuchus a genus of crocodilians in the family Erythrosuchidae. Well-known from several specimens, *Shansisuchus* was about 6 feet long. China, Middle Triassic.

Shantungosaurus a genus of hadrosaurid dinosaurs in the subfamily Saurolophinae. It is known from several partial skulls and skeletal remains, with a long, square snout. As long as 54 feet and weighing 15–16 tons, it is the largest-known hadrosaurid and one of the largest ornithischians. China, Late Cretaceous, about 78 Ma.

Sharktooth Hill one of the largest bone beds, a densely packed layer of fossils dated at 15 Ma. The site has yielded 40-foot *Carcharodon megalodon* remains, mainly teeth, and thousands of other marine species, as well as some terrestrial tapirs and ancestral horses. The remains were deposited over a period of about 700,000 years along the southeastern shore of the Temblor Sea, which covered California's long inland valley. United States, middle Miocene.

Sharovipteryx a genus of small gliding reptiles in the order Protorosauria. Known from one specimen found in the Madygen Formation of Kyrgyzstan in 1965 and dated at 225 Ma, it is especially notable for the membrane attached to its elongated hindlimbs and not to the pectora girdle. Kyrgyzstan, Late Triassic.

Shastasaurus a genus of ichthyosaurs in the family Shastasauridae. Known from specimens in California, Oregon, British Columbia, and China, the type species is *S. pacificus*. Since *Shastasaurus* is very different from other ichthyosaurs found in North America, it is one of the many kinds of evidence of the degree to which terranes of western North America have originated in the Pacific Ocean and been accreted by tectonic forces to the North American continent. North America and Asia, Late Triassic, 236–204 Ma.

Shipworm see **Teredinidae.**

Shonisaurus a genus of very large ichthyosaurs in the family Shonisauridae. Possibly the longest marine reptile known, it was bulky and dolphin-shaped, with a long, thin snout. It is known primarily from a bone bed in the Luning Formation in Nevada that contains more than 30 relatively complete specimens, all lying in the same position; the causes of their death are uncertain. The largest-known ichthyosaur is *S. sikanniensis*, an almost complete 68-foot specimen at the Royal Tyrrell Museum in Alberta; its placement is contentious, with some classifying it in the Shastasauridae. A 2016 discovery of a 3-feet-long jawbone in England is estimated to have belonged to a larger ichthyosaur similar to *Shonisaurus*, perhaps more than 80 feet long. North America and Europe, Late Triassic, 225–210 Ma.

Shrews see **Soricidae**.

Shumardiidae a family of minute, blind trilobites in the order Ptychopariida. About 5 mm long, they had a semicircular glabella with deep furrows and conspicuous lateral lobes. Global distribution, late Cambrian to Late Ordovician.

Shunosaurus a genus of basal eusauropod dinosaurs. A medium-sized sauropod, *Shunosaurus* is variously estimated at between 31 and 36 feet long, and it probably weighed about 3 tons. Its neck was relatively short, and it had a spiked club at the end of its tail. China, Middle Jurassic, 170 Ma.

Shuotherium a poorly known genus of Mesozoic mammals in the clade Yinotheria and family Shuotheriidae. Known from several dental fragments, it shares characteristics with monotremes and eutherians. The Shuotheriidae seem to be the only yinotherians of the Northern Hemisphere. England and China, Middle to Late Jurassic.

Shuvosaurus see ***Effigia*.**

Siamopithecus eocaenus a genus of primitive anthropoid primates in the family Amphipithecidae, found in the 1990s in Thailand. Reconstructions based on skull, jaw, and dental fragments indicate similarities to *Aegyptopithecus* and *Pondaungia*. Late Eocene.

Siberian Traps an area of lava flows, about 870 miles in diameter, northeast of Lake Baikal in Siberia. The eruptions occurred over a period of less than 1 million years, beginning about 248 Ma, and have been intensively studied because their date is so close to the end of the Permian. Some researchers believe the eruptions may be related to the causes of the great extinction that occurred then.

Sidneyia a monospecific genus of flattened stem arthropods of the Burgess Shale fauna. From 2 to 5 inches long, *S. inexpectans* is one of the larger arthropod-like animals at the site. Its glabella was wide and shaped like a ram, and it probably preyed on trilobites, brachiopods, and hyoliths. Canada, middle Cambrian, 508 Ma.

Sigaloceras calloviense a species of large ammonoids in the order Ammonitida and family Kosmoceratidae. About 8–10 inches high and 4 inches wide, it is prominent near the top of the Kellaways Formation of England, which gave its name to the Callovian Age of the Middle Jurassic. Europe, 164 Ma.

Sigillaria "seal-marked," a genus of large lycopodiophyte trees in the order Lepidodendrales. Ranging from 50 to 100 feet high, *Sigillaria* has leaves growing directly from the trunk and branches. The leaves are indistinguishable from those of the related genus *Lepidodendron*, but the leaf-scars are arranged in parallel vertical rows instead of the spiral arrangement of *Lepidodendron*. Fossils of the bark are classified as the form genus *Knorria*. Global distribution, Devonian to Permian.

Silesauridae a family of archosaurian reptiles in the clade Dinosauriformes. The family includes several genera that seem close to the line of descent to dinosaurs, such as *Silesaurus*, *Asilisaurus, Diodorus, Eucoelophysis, Lewisuchus*, and probably *Agnosphitys*. South America, Africa, United States, and Europe; Middle to Late Triassic, 245–203 Ma.

Silesaurus a genus of dinosauriform reptiles in the family Silesauridae. The type genus of the family, *Silesaurus* bears several dinosaurian features and is known from two dozen specimens found at a site in Silesia. Poland; Carnian, Late Triassic, 230 Ma.

Silurian the third period of the Paleozoic Era, from 444 to 416 Ma. The beginning of the period saw a generally rapid recovery from the effects of the end-Ordovician extinction. Agnathans and placoderms were the most abundant vertebrates, but by the end of the period, all principal groups of vertebrates had evolved. Stromatolite and coral reefs covered large areas of the shallow seas; Silurian strata are mostly calcitic, with some sandstones and graptolite shales. The first vascular plants

appeared in the middle Silurian, and plants such as rhyniophytes and club mosses increased their colonization of the land, creating a great diversity of new terrestrial ecosystems.

Silvacola acares a species of very small hedgehogs in the extant family Erinaceidae, found in 2014 in northern British Columbia. It is only 2–3 inches long but is otherwise similar to modern hedgehogs. Whether *Silvacola* had spines cannot be determined from the specimens. Canada, early Eocene, 50 Ma.

Silvanerpeton miripedes a species of reptiliomorphs considered an advanced reptile-like amphibian. Probably a basal tetrapod, it is known from a partial skeleton and other fragments found in the East Kirkton Quarry. It was about 16 inches long, had large eye orbits, and had only five digits. Scotland, Early Carboniferous, 338–334 Ma.

Silvisaurus condrayi a species of nodosaurs in the subfamily Nodosaurinae. Estimated at 13 feet long, it is known from one partial skeleton: a mandible, several vertebrae, several other bones, and some plates and spikes from its body armor. Found in an exposed and disturbed riverbed in north-central Kansas, it is thought to be the only dinosaur that inhabited the area. United States, Late Cretaceous, 96–94 Ma.

Simiolus a genus of stem-catarrhine primates in the family Dendropithecidae. Five species are known, including *S. minutus*, which is estimated to have weighed 8 pounds and seems to be the smallest ape yet discovered. *S. minutus* is known only from four partial teeth. East Africa, early to middle Miocene.

Simocetus rayi a species of toothed whales, considered the earliest odontocete. Known only from a single skull found in Oregon, it has facial features similar to dolphins and is called "pug-nosed whale." United States, early Oligocene.

Simoedosauridae see **Choristodera.**

Simoliophiidae a small family of limbed marine snakes in the suborder Serpentes; synonym Pachyophiidae. It includes *Haasiophis, Eupodophis*, and a few other small basal snakes. Lebanon and Morocco, Late Cretaceous, 99–92 Ma.

Simosuchus clarki an unusual species of crocodilians known only from the Maevarano Formation of Madagascar. Less than 3 feet long and weighing about 20 pounds, it was well-armored by a dense covering of osteoderms from its small head to its stubby tail. *Simosuchus* had a short, deep skull with a very blunt snout, which gives it the name "pug-nosed." Its teeth are flattened, with some denticles on the blunt crown, indicating that it may have been herbivorous. The short tail suggests that it was not a good swimmer and made its living mainly on land. Madagascar, late Cretaceous, 70–66 Ma.

Sinoceratops an Asian genus of short-frilled ceratopsid dinosaurs in the subfamily Centrosaurinae. They were herbivorous, medium-sized, and quadrupedal and are still the only ceratopsians known from Asia. Two species found in 2008 have been identified as *S. zhuchengensis* and *S. formosensis*. China, Late Cretaceous, 72–66 Ma.

Sinoconodon a genus of early mammaliamorph in the clade Cynodontia. One of the earliest cynodonts, it is probably ancestral to *Morganucodon*. Although similar in many ways (such as polyphyodonty) to the nonmammalian synapsids, it also has several characters that mark it as a basal mammal (especially in the jaw joint). China, Early Jurassic, 193 Ma.

Sinodelphys szalayi a species of shrew-like metatherian mammals, the earliest-known mammal to be more closely related to marsupials than to placentals. Known from one well-preserved specimen found in the Yixian Formation, it was scansorial, about 6 inches long, fur-bearing, and it probably weighed about one ounce. China, Early Cretaceous, 125 Ma.

Sinopterus a genus of small pterodactyloid pterosaurs in the family Tapejaridae. Dated at 120 Ma, it had a wingspan of almost 4 feet. The first tapejarid found outside Brazil, *Sinopterus* is known from three specimens found in the Jiufotang Formation. China, Early Cretaceous.

Sinornithosaurus millennii a species of theropod dinosaurs in the family Dromaeosauridae. It was turkey-sized and had birdlike features and short, downy proto-feathers, but probably did not fly. It is notable for single large claws on hind feet and long claws on its arms, possibly poisonous. Jehol Biota, China, Early Cretaceous, 120 Ma.

Sinosauropteryx prima a species of small theropod dinosaurs in the family Compsognathidae. One of several feathered dinosaurs in the Jehol Biota, it was about 3 feet long and similar to *Compsognathus*. It seems to have had rings of different-colored feathers on its tail and a colored stripe across its eyes. Researchers base this conclusion on melanosomes, cells that contain the pigment melanin. The color itself is not visible in the fossil, but electron microscope analysis of melanosomes in the follicles gives indirect evidence of a russet color. The feathers were as long as 1.5 inches and were evidently bristly like those of the modern kiwi. *Sinosauropteryx* was about 3 feet long but weighed only 2–5 pounds; it had 64 vertebrae in its tail, more than any other theropod. China, Early Cretaceous, 127–125 Ma.

Sinotubulites a genus of wormlike animals notable for its cone-in-cone shell. It was one of the earliest-known shelled animals, slightly later than *Cloudina*. See also ***Namacalathus*** and ***Namapoikia***. China and Mexico, early Cambrian 542–530 Ma.

Sinraptor a genus of theropod dinosaurs in the superfamily Allosauroidea and family Metriacanthosauridae. Known from two incomplete skeletons with skulls, it grew up to 25 feet long and 10 feet high. *Sinraptor* was near the top of the food chain but was smaller than the contemporary carnivore *Yangchuanosaurus***.** China, late Jurassic, 160 Ma.

Sinraptoridae see **Metriacanthosauridae**.

Siphonia a genus of demosponges in the polyphyletic order Lithistida and extinct family Hallirhoidae. Globular, cylindrical, or pear-shaped, they were anchored to the seafloor by a stalk and a root system or holdfast. The name refers to the main feeding tube, which runs through almost the whole length of the body. Europe, Early Cretaceous to late Eocene.

Siphonodella a genus of conodonts important in the biostratigraphy of the Late Devonian and Early Carboniferous. Global distribution, 376–354 Ma.

Siphonodella sulcata a species of conodonts whose first appearance marks the beginning of the Tournaisian, the first age of the Carboniferous, at 358.9 Ma; France.

Siphonotretida a Paleozoic order of brachiopods in the class Lingulata. It includes only the single family Siphonotretidae. Global distribution, early Cambrian to middle Permian.

Siphonotretidae a small family of inarticulate brachiopods in the order Siphonotretida and superfamily Siphonotretoidea. Similar to the Obolellida and extant Acrotretida, they are characterized by a teardrop-shaped, chitinophosphatic shell and an elongate or apical pedicle valve. Global distribution in the Ordovician; middle Cambrian to middle Permian.

Sirenia an extant order of fully aquatic mammals, some freshwater, placed in the clade Tethytheria. The earliest sirenian is ***Pezosiren***, *q.v.* Transitional sirenians are known from the Eocene families Prorastomidae and Protosirenidae, and extinct genera of the extant families Dugongidae and Trichechidae are known from the Miocene. Global distribution, early Eocene to Recent.

Sirilorica a poorly known genus of invertebrates in the clade Scalidophora, similar to priapulid worms. They were elongate and 1–3 inches long and covered with chitinous plates called loricae. Known only from Sirius Passet, Greenland, early Cambrian.

Sirius Passet a locality in Greenland that has produced soft-bodied fossils similar to those of the coeval Chengjiang biota, known especially for ***Halkieria***, *q.v.* The Sirius Passet strata are dated between 523 and 518 Ma. Early Cambrian, ca. 520 Ma.

Sister group a phylogenetic term referring to the most closely related taxa in an evolutionary lineage, those more closely related to each other than either is to other taxa. The term is used most often in relation to species and genera, but it may also designate most closely related clades as sister clades.

Sivapithecus a genus of hominoid primates in the subfamily Ponginae, known from fossils found at several sites in Asia; formerly called *Ramapithecus* and *Brahmapithecus*. About 5 feet long, they probably spent some time in trees but were mainly ground-dwelling. There is still disagreement as to their place in hominoid evolution, but they may be close to the ancestry of modern orangutans. India, middle to late Miocene, 12.5–8.5 Ma.

Sivatherium a genus of artiodactyl mammals in the family Giraffidae. It was similar to the modern okapi but larger, about 10 feet high and 7 feet at the shoulder, weighing at least half a ton. It had a pair of wide, antler-like ossicones at the back of its skull and a smaller pair above its eyes. Africa and India, Pliocene to about 8000 years ago.

Skolithos an ichnogenus of burrows as wide as 1.6 inches, found mainly in marine and sometimes in freshwater strata. The often-vertical burrows are straight, helical, or slightly curved. These trace fossils are made by phoronids, worms, insect larvae, other arthropods, and even small vertebrates. Ediacaran to Recent.

"Small, shelly fauna" a "catch-all name that spells frustration" according to Stephen Jay Gould. The phrase refers to an enigmatic assemblage of spines, plates, caps, and cups that represent the first steps toward hard skeletons in animals. Occurring globally from the end of the Ediacaran into the early Cambrian, these fragmentary bits and pieces have long been a puzzle, but whole specimens have now been discovered of some of the animals that bore the fragments in life. See, for example, ***Microdictyon sinicum, Sinotubulites,*** and ***Cloudina*****.**

Smilodectes a genus of small adapiform primates in the order Strepsirrhini and subfamily Notharctinae. The scansorial *Smilodectes* weighed 4–6 pounds and is distinguished by a relatively short snout. United States, early Eocene.

Smilodon "knife-tooth," a genus of cats in the subfamily Machairodontinae. It was one of several genera of large saber-toothed cats that flourished in the Pliocene and Pleistocene but disappeared about 10,000 years ago. Global distribution except Australia. See also ***Megantereon, Homotherium***, **Machairodontinae,** and ***Thylacosmilus*****.**

Smilodon fatalis the species of saber-toothed cats found in the La Brea Tar Pits in Los Angeles; middle Pleistocene to about 11,000 years ago.

Smilodon gracilis an early California sabertooth, Pliocene to about 1 Ma.

Smilodon populator a South American saber-toothed cat, considered the largest-known felid at 500–800 pounds. It was widespread in South America in the late Pleistocene until about 10,000 years ago.

Smith, William An English geologist, Smith is considered the founder of biostratigraphy for his groundbreaking geologic map of England of 1815, which revolutionized the study of layers of rock, brilliantly combining paleontology, petrology, and geology, comparing fossils in widely separated rock outcrops to understand the strata underlying the Earth's surface. By establishing the principle of faunal succession, Smith's work immediately inspired widespread use of his techniques.

Solanaceae the nightshades, a large extant family of plants in the order Solanales. A 2017 description of early Eocene (52 Ma) lantern fruits in the genus *Physalis* reports the earliest-known occurrence of the family, in Patagonia before the breakup of South America from Antarctica. Global distribution, Eocene to Recent.

Solenopora a disputed genus of calcite-secreting organisms, traditionally classified as algae in the division Rhodophyta and extinct family Solenoporaceae. However, most specimens are now recognized as chaetetid sponges. They generally occur as nodular masses, while some late Paleozoic and Mesozoic forms occur as encrusting mats. They appeared in the Cambrian, and some forms may still be extant. A banded pink form of the Jurassic that is generally considered an alga, *S. jurassica*, is also called *Neosolenopora* and commonly referred to as "beetroot." Its striking color results from the presence of a boron-containing organic compound called a borolithochrome, which is identified by biochemical molecular analysis. Global distribution, Cambrian to Cretaceous(?).

Solitaire see ***Pezophaps***.

Solite Quarry an important Triassic Konservat-Lagerstatten that straddles the border between Virginia and North Carolina, noted especially for insects and small reptiles. Its lakebed deposits were laid down over a period of less than 50,000 years. United States, Late Triassic, late Carnian to Norian, 227 Ma.

Solnhofen Limestone a Late Jurassic Konservat-Lagerstatten in Bavaria, where several quarries produce lithographic limestone, with fossils of the best quality coming from those near the towns of Solnhofen and Eichstätt. The extremely fine-grained limestone layers of the Solnhofen Formation were laid down in a protected lagoon on the northern edge of the Tethys Sea over a period of half a million years. The stagnant lagoon contained anoxic and hypersaline areas with few benthic organisms, and most of the 600 species of fossils are allochthonous, probably washed into the lagoon by storms. Several crustacean fossils lie at the end of "death trail" trackways, one 30 feet long (see ***Mesolimulus*** and ***Mecochrinus***). Only one definitive dinosaur, *Compsognathus*, is known here; it has several skeletal similarities to *Archaeopteryx*, the best-known of the Solnhofen fossils. Marine vertebrates

such as ichthyosaurs are known only from poorly preserved fragments, having reached the lagoon through the coral reefs at its edge during severe storms. Other well-preserved fossils include pterosaurs, some with toe-webbing and hairlike covering of wing membranes intact, fish, amphibians, insects, and many arthropods. Germany, Late Jurassic (Kimmeridgian, 150 Ma).

Solo man see **Ngandong fauna**.

Sonninia a genus of ammonoids in the family Sonniniidae; (formerly *Euhoploceras*). Global distribution, Middle Jurassic, 172–168 Ma.

Sonorasaurus thompsoni a mid-Cretaceous sauropod of North America, a species of large sauropod dinosaurs in the family Brachisauridae. Notable for its extremely long neck, *Sonorasaurus* grew as long as 55 feet and 30 feet high, its neck evidently almost as long as the rest of its body and tail. Sonora Desert, Albian to Cenomanian.

Soomaspis a monospecific genus of trilobite-like arthropods in the order Nektaspida and family Liwiidae. Isopygous and eyeless, and with only three thoracic segments, *S. splendida* resembles a soft-bodied agnostid trilobite. Known only from the Soom Shale of South Africa, Late Ordovician.

Soom Shale an important Late Ordovician Konservat-Lagerstatten near Cape Town, South Africa. Several sites contain exceptionally well-preserved fossils in cold-water deposits of the Upper Ordovician, 445–444 Ma. Although the formation is unusual for the almost complete absence of benthic organisms, its biota includes several organisms familiar from the Cambrian Lagerstätten as well as some that became more prominent later in the Paleozoic, such as the eurypterid *Onychopterella*. Among other important specimens are the conodont *Promissum pulchrum* and the nektaspid *Soomaspis*, as well as brachiopods, lobopods, orthocone cephalopods, and chitinozoans.

Soricidae the shrews, an extant eulipotyphlan family of small, mouselike mammals in the clade Soricomorpha. Mainly insectivorous, they first appeared in Asia in the Eocene and have diversified worldwide. The earliest-known is *Soricolestes*, from the middle Eocene of Mongolia.

Soricomorpha a clade of small eulipotyphlan mammals generally considered to include the shrews and moles. Global distribution, Eocene to Recent.

Spatangoida the heart urchins, an extant order of atelostomate echinoids, recognized by an oval shape and a deep groove into the mouth. Global distribution, Early Cretaceous to Recent.

Speciation development of new species through lineage splitting, resulting in reproductively isolated branches.

Species (1) biological species concept: a group of actually or potentially interbreeding organisms that are almost completely isolated reproductively from other organisms, exchanging only a few genes. (2) evolutionary species concept: a single lineage of ancestor-descendant populations that maintains its own identity distinct from other lineages. The lineage may be recognized by phenotypic and genotypic characteristics.

Species duration The length of time that a species persists varies widely, with some long-lived species lasting many millions of years, but the average duration is generally taken to be about 4 million years.

Speciose species-rich, containing many species.

Sphaeractinoidea Mesozoic marine hydrozoans possibly related to the stromatoporoids and the spongiomorphs. They have long been called "Mesozoic stromatoporoids," but the discovery of spicules in some species has resulted in those species being reclassified as demosponges and raised the possibility that all sphaeractinoids may eventually be reclassified.

Sphaerirhynchia a genus of articulate brachiopods in the extant order Rhynchonellida and extinct superfamily Rhynchonelloidea. Strongly biconvex and almost spherical, less than an inch in diameter, they attached to the soft substrate with a functional pedicle. Global distribution, Silurian and Devonian.

Sphenacodon "wedge-point tooth," the type genus of the synapsid family Sphenacodontidae. Between 6 and 10 feet long, *Sphenacodon* was slightly smaller than its cousin *Dimetrodon* and had only a low sail about a foot high. United States, Late Pennsylvanian to middle Permian.

Sphenacodontidae a family of large, advanced pelycosaurian synapsids with relatively long and narrow snouts and skulls. Several had tall, sometimes greatly elongated neural spines. The most familiar sphenacodontid is *Dimetrodon*, which is well-known for its sail more than 3 feet high. North America and Europe, Late Carboniferous to middle Permian.

Spheniscidae the penguins, an extant family of large flightless birds of the Southern Hemisphere. They first appeared in the middle Eocene and diversified rapidly. Notable for having retained the bone structure and musculature of flying birds despite being flightless, penguins adapted these flight structures to swimming, essentially flying underwater. Middle Eocene to Recent.

Sphenodon "wedge tooth," the tuatara, an extant genus of lizard-like reptiles in the family Sphenodontidae, represented by two species in New Zealand, *S. punctatus* and *S. guntheri*. It grows as long as 2.5 feet and weighs up to 3 pounds. New Zealand, Miocene to Recent.

Sphenodontidae an extant family of lizard-like reptiles in the order Rhynchocephalia. Sphenodonts were numerous in the Jurassic but are represented today by only one genus, the tuatara of New Zealand (*Sphenodon*); see also ***Planocephalosaurus***. Global distribution, Triassic to Recent.

Sphenophyllales "wedge leaf," an extinct order of articulate vascular plants in the class Equisetopsida, related to the modern horsetails. Small and slender, they grew up to about 3 feet, with jointed stems and linear, forked, or wedge-shaped leaves. They are common as fossils from the Carboniferous and early Permian. Global distribution, Early Devonian to Late Triassic.

Sphenophyta see **Equisetopsida**.

Sphenopteris a form genus of leaves from late Paleozoic and Mesozoic plants. It is known generally from seed plants such as *Lyginopteris* but also from some spore-producing ferns. Global distribution, Devonian to Late Cretaceous.

Sphenosuchia an order of basal crocodylomorph reptiles. Between 1 and 2 feet long, they were fast runners, with an upright posture and long, slender legs. The monophyly of the order is in question. Global distribution, Middle Triassic.

Sphinctozoans a polyphyletic group of calcified sponges, most of which grow as a series of chambers, one on top of the next. The chambered sphinctozoans are considered one of the hypercalcified sponges. They originated in the Cambrian and flourished in the late Paleozoic and the early Mesozoic. They are absent from the fossil record since the Late Cretaceous, but a single surviving species, *Vaceletia crypta*, was discovered in Australia in 1977. See also ***Girtyocoelia***. Global distribution, Cambrian to Recent.

Spiclypeus shipporum a species of ceratopsid dinosaurs in the subfamily Chasmosaurinae. Known from a partial skull and bones of the spine, legs, and hips, found in Montana. It was about 15 feet long and weighed up to 4 tons, a medium-sized ceratopsian. Like other chasmosaurs, it had a large and highly ornamented neck frill. United States, Late Cretaceous, 76–75 Ma.

Spicule a pointed mineral structure, most often of silica or calcium carbonate, that is part of an animal's skeleton, as in some sponges and brachiopods.

Spiders see **Araneae**.

Spinicaudata see **Branchiopoda**.

Spinosaurus aegyptiacus the type species of a genus of very large carnivorous dinosaurs characterized by sturdy 6-foot-long vertebral spines and by crocodile-like teeth as long as 7 inches. Although it is known from only partial remains, it may

have been the largest-known carnivore at 36–50 feet long. Its long snout contained dozens of sharp, conical teeth, resembling those of modern crocodiles. Study of various fossils, including a partial skeleton from the Kem Kem Beds — described in 2013 — seems to prove that *Spinosaurus* spent a large part of its life in North African rivers, preying on the numerous large species of fish and turtles. It was discovered about 1913 by Ernst Strömer, who may have suspected its riverine habit but could not prove it. See also ***Bahariasaurus, Baryonyx, Carcharodontosaurus, Suchomimus***, and **Strömer's Riddle**. North Africa, Early to Late Cretaceous, 112–94 Ma.

Spiriferida an order of articulate brachiopods in the class Rhynchonellata. Strongly ribbed and either punctate or impunctate, spiriferides are notable for a long, straight hinge line that is the widest part of the body, so that the animal appears to be winged. The name of the order refers to the laterally directed spiral brachidia, which support the lophophore. The Spiriferida appeared in the Cambrian, were still rare through the Silurian but widespread in the Devonian and Carboniferous, survived the end-Permian extinction, and persisted to the Early Jurassic.

Spiriferidina a suborder of articulate brachiopods. The larger of the two suborders in the order Spiriferida, it is marked by strong ribbing and a wide hinge line. See also **Delthyridina**. Global distribution, Late Ordovician to Triassic.

Spiriferina walcotti a species of articulate brachiopods in the order Spiriferinida. Characterized by a broad, ribbed shell with a wide hinge line and folds at the edge, it was 1–2 inches wide with faint concentric growth lines. Europe, Early Jurassic.

Spiriferinida an order of later articulate brachiopods in the class Rhynchonellata, similar to Spiriferida but generally smooth-shelled; global distribution, Early Devonian to Early Jurassic.

Spirulida an order of coleoid cephalopods with only one extant genus, the deep-water *Spirula*, and several extinct genera possibly dating back as far as the Late Carboniferous. They differ from most coleoids by having a light external shell in addition to a small internal shell. Global distribution, Late Carboniferous or Late Jurassic to Recent.

Spondylus an extant, large, and diverse genus of spinose bivalve mollusks in the family Spondylidae and in the same superfamily as scallops, the Pectinoidea. It cements itself to rocks and is often called "spiny oyster," although unrelated to oysters. Up to 4 inches wide, it has several eyes around the edges of the shell. Global distribution, Middle Triassic to Recent.

Sponges see **Porifera**.

Spongiomorphidae the single family of colonial hydrozoans in the extinct order Spongiomorphida. Their massive colonies are characterized by longitudinal rods perpendicular to the growth surface and connected by horizontal bars parallel to the surface. Global distribution, Late Permian to Eocene.

Spriggina an enigmatic genus of soft-bodied organisms known definitively only from the Ediacara Hills. From 1 to 2 inches long, it was multi-segmented, with a small, horseshoe-shaped head. Its fossils superficially resemble a wormlike arthropod, but several characters seem to mark it as un-arthropod; it also resembles sea pens and some rangeomorphs. Australia, 560 Ma.

Springtails see **Collembola**.

Squalodontidae a possibly polyphyletic family of large-toothed whales in the superfamily Platanistoidea. Although poorly understood, they seem to be intermediate between the Archaeoceti and the Odontoceti. The type genus *Squalodon* is the only unquestioned member of the family. Global distribution, Oligocene to Pleistocene.

Squaloraja polyspondyla a species of chimaeriform fish in the family Squalorajidae that seems to be transitional between sharks and rays. It is known only from one specimen collected by Mary Anning in Lyme Regis and one from Italy. England and Italy, Early Jurassic.

Squamata an order of reptiles in the subclass Lepidosauria; its sister group is the Rhynchocephalia. The second-largest order of vertebrates, after the perciform fish, the squamates include the snakes (Ophidia), lizards (Lacertilia), and worm lizards (Amphisbaenia). The squamates probably developed in the late Permian and diverged from rhynchocephalians in the Early Triassic, but their early fossil record is still sparse. For the earliest known, see ***Megachirella***. Global distribution, Middle Triassic to Recent.

Staffellidae a family of small benthic, semi-infaunal foraminiferans in the superfamily Fusulinoidea, related to the Ozawainellidae. The test is spherical to discoidal, with sharply arched septa. Global distribution, Late Carboniferous to late Permian.

Stage the term for a geochronological interval, referring to dates of geological formations.

Stagonolepis a genus of herbivorous aetosaurian reptiles in the family Stagonolepididae. Quadrupedal and slow-moving, it was about 10 feet long and well-armored, with osteoderms covering most of its body. *Stagonolepis* had no teeth at the front of its mouth but had cheek teeth adapted for chewing vegetation. Europe and possibly North and South America, Late Triassic, 237–227 Ma.

Staphylinidae the rove beetles, the largest family of beetles, in the order Polyphaga. Staphylinids are carnivorous or omnivorous scavengers. Probably the oldest is *Leehermania prorova*, found in the Solite Quarry of the eastern United States and described in 2012. Global distribution, Late Triassic to Recent.

Staurikosaurus a genus of early theropod dinosaurs in the family Herrerasauridae. Dated at 225 Ma, it is one of the earliest-known dinosaurs. It was 7 feet long and weighed about 66 pounds. Brazil, Late Triassic.

Stauropteridae a group of enigmatic ancestral ferns usually considered cladoxylopsids. Poorly known, they had forked, spore-bearing branches, similar to the ancestral *Cooksonia* of the Silurian. Cosmopolitan, Late Devonian to Late Carboniferous.

Stegocephalians a paraphyletic group of choanatan lobe-finned animals. They were formerly considered rhipidistian fish but are now identified as tetrapods (such as *Tiktaalik* and *Ventastega*), transitional forms leading to the first terrestrial animals. Cosmopolitan, Middle to Late Devonian.

Stegoceras a poorly known genus of medium-sized pachycephalosaurid dinosaurs. Estimated at 7 feet long and 60–80 pounds, it is known mainly from several almost complete skulls with a thick dome. Canada and probably United States, Late Cretaceous, 78–74 Ma.

Stegodontidae a family of proboscidean mammals in the extinct suborder Mammutoidea, considered by some to be a subfamily in the Elephantidae. They had low-crowned teeth with thick enamel but like modern elephants had lost their lower tusks. Africa and Asia, middle Miocene to late Pleistocene.

Stegosauria a suborder of medium-sized herbivorous ornithischian dinosaurs. They were well-armored, with a row of plates along the spine, scutes covering the body, and terminal spikes on the tail. The head was small and narrow, and they had long hindlimbs but were quadrupedal. Global distribution, Early Jurassic to Early Cretaceous, 169–125 Ma.

Stegosauridae a family of large ornithischian dinosaurs in the suborder Stegosauria. The Stegosauridae were larger than other stegosaurs, the type genus *Stegosaurus* weighing more than 5 tons. North America, Europe, Asia, and Africa; Middle Jurassic to Early Cretaceous, 165–136 Ma.

Steinheim skull a fairly well-preserved hominin skull without the lower jaw, found at Steinheim, Germany. It has characteristics of Neanderthals and of *Homo heidelbergensis* and is estimated to be between 250,000 and 350,000 years old.

Stem group a paraphyletic grouping of organisms at the base of a lineage, consisting only of extinct species and excluding all members of the crown group.

Steneosaurus a genus of thalattosuchian crocodylomorphs in the family Teleosauridae. Between 7 and 17 feet long, it swam in shallow seas in the middle of the Mesozoic. The species in the genus provide an example of niche partitioning, being divided into two groups, one with short, broad jaws and the other with long, very narrow jaws, similar to the modern gharial. Especially good specimens of the latter species are known from the Holzmaden Shale. Europe and Madagascar, Early Jurassic to Early Cretaceous.

Stenohaline not tolerant of a wide range of salinity. Trilobites and brachiopods, for example, are stenohaline and less able to tolerate changes in salinity than bivalves, which are generally more euryhaline.

Stenolaemata the oldest class of marine bryozoans. With sac-shaped, tubular, or conical exoskeletons, stenolaemates were the dominant bryozoans throughout the Paleozoic, contributing to reefs in many places. One order, the Cyclostomatida, is still extant; the Cystoporata and Cryptostomata became extinct at the end of the Permian and the Trepostomata in the Triassic. See also **Gymnolaemata**. Global distribution, Early Ordovician to Recent.

Stenophlebiidae a family of damsel-dragonflies in the order Odonata. Medium-sized to large, they are distinguished by their wing venation pattern and long, slender wings. Europe, Asia, and South America; Late Jurassic to Early Cretaceous.

Stenopterygius "narrow wing," a genus of thunnosaurian ichthyosaurs known from well-preserved specimens from Holzmaden and other Lower Jurassic sites. Up to 12 feet long, it had a long, narrow beak and long, thin pectoral fins. A famous Holzmaden specimen is a mother and fetus which died before childbirth, with the fetus in a position to be born tailfirst. Europe, Early Jurassic.

Stensioellida a monospecific order of primitive fish, generally considered the most primitive placoderms. The order consists of one species, *Stensioella heintzi*, known only from the Hunsrück Slate. It has a whiplike tail and large pectoral fins, and its elongate body has no large bony plates but is armored by a mat of small dermal tubercles. Germany, Early Devonian.

Stenurida a small order of primitive asterozoan echinoderms in the class Ophiuroidea. This group of brittle stars includes widely disparate families and may be polyphyletic. Cosmopolitan, Early Ordovician to Late Devonian.

Stephanoceras a genus of large ammonoids in the order Ammonitida and family Stephanoceratidae. The type genus of the family, it is evolute, has a small number of tubercles, and is notable for its bulk, often being 11 inches high and 2–3 inches wide. North America, Africa, and Asia; Middle Jurassic, 172–168 Ma.

Stephanodiscus yellowstonensis a species of diatoms in the order Thalassiosirales with a unique history. Recent research shows that it evolved within a short span of time in the Yellowstone area of Wyoming, between 12,000 and 8000 years ago. Once found in many lakes of the area, it is now restricted to Yellowstone Lake. It has not evolved further in the last 8000 years and seems to be becoming increasingly less abundant.

Stereom the spongelike network of calcium carbonate crystals that composes the body tissue of all echinoderms.

Stereospondyli a large suborder of late temnospondyl reptiles, including the Capitosauroidea, Plagiosauroidea, Trematosauroidea, and several smaller groups. Mostly aquatic and distinguished by a broad, flat head, the largest were about 7 feet long. They were among the last of the temnospondyls, known only from Gondwana up to the end of the Permian but then radiating worldwide in the Triassic. Late Permian to Early Cretaceous.

Steropodon one of several extinct genera of monotremes in the family Steropodontidae. Known only from a single jawbone, it had teeth and is estimated at 2 feet long, large for a Mesozoic mammal. Closely related to the modern platypus (*Ornithorhynchus anatinus*), it may also be related to the smaller and slightly earlier *Teinolophos*, which is known only from dental fragments. New South Wales, Australia, Early Cretaceous, 110–105 Ma.

Stethacanthus "chest spine," a genus of Devonian sharks in the order Symmoriida, notable for a mysterious first dorsal fin on the male. It is a flattened area covered with dermal denticles, looking like a narrow, toothed anvil, and its purpose is unclear. *Stethacanthus* is named for the long extensions from its pectoral fins, called fin whips. United States, Europe, and Asia; Late Devonian to Early Carboniferous.

Sthenurus "strong tail," a genus of kangaroos in the family Macropodidae and extinct subfamily Sthenurinae. Short-faced and with a tail shorter but stronger than modern kangaroos, they grew as long as 10 feet and weighed more than 500 pounds. Australia, Pliocene to Pleistocene, becoming extinct later than 19,000 years ago.

Stigmaria a form genus of the rooting structures of lycopsid trees such as *Lepidodendron* and *Sigillaria*; global distribution, Carboniferous.

Stipe the branch of a graptolite, to which the individual thecae are attached; also, the stem of algae connecting the holdfast to the upper parts.

Stolonoidea a group of encrusting or sessile animals generally considered graptolites, but possibly belonging to the pterobranch family Rhabdopleuridae; global distribution, Ordovician.

Straparollus see ***Euomphalus***.

Stratigraphy the descriptive study of rock strata and interpretation of geological history, including deposition, relative age, and correlation between exposed strata that may be separated by great distances. See also **biostratigraphy** and **key bed**.

Strawberry Bank a Lower Jurassic Lagerstätte in Somerset, England. It is one of three Lagerstätten dated near the boundary of the Pliensbachian and Toarcian Ages of the Early Jurassic, along with the well-known Holzmaden deposits in Germany and the recently developed Ya Ha Tinda site in Canada. Strawberry Bank is especially notable for its nearshore deposits containing 20 species of insects as well as its specimens of nektic organisms (especially ichthyosaurs, fish, and cephalopods). It differs from other sites also in having predominantly three-dimensional specimens inside calcareous nodules. England, Early Jurassic, 183 Ma.

Strelley Pool Chert a rock formation in Western Australia dated at 3.4 billion years old. Some of its strata contain features that seem to be stromatolites, which would be the oldest fossils known if confirmed.

Strepsirrhini a suborder of primates that includes the lemuroids, galagos, and lorises, and their extinct adapiform primate relatives; formerly called Prosimii. They are distinguished from haplorrhines by the moist area around their nostrils; see also ***Haplorrhini.*** The strepsirrhines were widespread in Laurasia from the Eocene to the Miocene but are now found only in tropical Asia and Africa. Early Eocene to Recent.

Strepsodiscus possibly one of the earliest mollusks, a genus of primitive snail-like mollusks generally considered bellerophontid gastropods. Two species are known, with an asymmetrical shell about an inch high. See also ***Chippewaella*** and **Bellerophontoidea.** North and South America and Antarctica, late Cambrian to Ordovician.

Streptelasma a genus of stauriid horn corals in the family Streptelasmatidae. From 1 to 2 inches long with a deep calyx, *Streptelasma* had a curved, funnel-shaped corallum with no dissepiments between the numerous septa. Global distribution, Early Ordovician to Late Devonian.

Streptognathodus isolatus a species of conodonts in the family Polygnathidae. Its first appearance, in Kazakhstan, marks the beginning of the Permian at 298.9 Ma. Several other species of *Streptognathodus* are important biostratigraphic markers for ages of the Late Carboniferous and early Permian. North and South America and Asia.

Streptospondylus "twisted vertebra," a genus of medium-sized theropod dinosaurs in the family Megalosauridae. One of the first dinosaurs to be discovered, its fossils were found in the late eighteenth century in France and described variously for several decades until finally recognized as dinosaurs. France, Middle Jurassic.

Stridulation see **Orthoptera**.

Strobilus a cone; a common form genus of many cone-bearing plants.

Stromatolites layered accretionary structures formed by microorganisms in a process of microbial growth, decomposition, and lithification. They accumulate grains of sediment of many kinds in biochemical films called laminae, whose morphology varies according to water depth and wave action. Some as much as 3.5 billion years old, they occur in varied shapes from conical to horizontal, often forming reefs. Global distribution, Archaean to Recent.

Stromatoporoidea a group of primitive reef-building organisms now generally considered poriferans, either demosponges or sclerosponges, but their precise affinities are still in dispute. See also **Sphaeractinoidea. C**osmopolitan, Precambrian to Cretaceous, but especially important reef-builders in the Silurian and Devonian.

Stromatoveris a genus of frond-like animals known only from Chengjiang. It seems closely related to Ediacaran organisms and is tentatively assigned to a new phylum, Petalonomae. China, early Cambrian, 520–516 Ma.

Strömer's Riddle the question why so many large predatory dinosaurs inhabited the riverine environments of North Africa in the middle of the Cretaceous although relatively few herbivores were present. Ernst Strömer, of the University of Munich, raised the question in the course of his extensive excavations in North Africa in the early twentieth century; most of his specimens were lost in a bombing raid on Munich in 1944. Some research between 2010 and 2014 indicates that the large carnivores were supported by a large population of gigantic aquatic animals, such as a variety of very large turtles, 8-foot lungfish, 13-foot coelacanths, and 25-foot sawfish. If further research confirms that *Spinosaurus* and other large predators did in fact spend most of their time in the water, the riddle may have been solved.

Stropheodonta a genus of small brachiopods in the family Leptostrophiidae, a characteristic strophomenid that is important in Devonian stratigraphy. Its brachial valve is slightly concave and brachial valve convex, both with fine ribbing; its hinge line is wide and straight. Global distribution, Silurian to Devonian.

Strophic of brachiopods, having a well-defined and elongated hinge line, as opposed to astrophic hinges, which do not have a well-defined hinge line but have the two valves hinged at a point. The most elongated strophic brachiopods may appear to have wings.

Strophomenata an extinct class of mostly articulate brachiopods in the subphylum Rhynchonelliformea. It is generally taken to include the orders Productida, Strophomenida, Billingsellida, and Orthotetida. Global distribution, Cambrian to Early Jurassic.

Strophomenida a large order of articulate brachiopods in the class Strophomenata, with global distribution. The Strophomenida are usually wider than long, with a strophic hinge line and one convex valve and the other flat or concave. Traditionally the order has included a wide range of diversity and been dated from the Ordovician to the early Jurassic. Some authorities now restrict it to fewer families and date its extinction in the Early Carboniferous.

Strunius a genus of unusual lobe-finned fish in the order Onychodontida. Only 4 inches long, *Strunius* had the articulated skull characteristic of the rhipidistians and the coelacanths. Its fins were not so muscular as those of other lobe-fins, being stiffened by bony rays like the fins of actinopterygians. Europe, Late Devonian.

Struthiomimus "ostrich mimic," a genus of medium-sized saurischian dinosaurs in the family Ornithomimidae. It was bipedal and birdlike, with a small, slender head and long neck. The type species, *S. altus*, was about 14 feet long and weighed about 330 pounds. Canada, Late Cretaceous, 78–68 Ma.

Struthiosaurus a basal genus of ankylosaurs in the family Nodosauridae. The smallest ankylosaur known, *Struthiosaurus* was 7 feet long and relatively lightly armored. It is known from several sets of partial remains found across Europe from Romania to France. Europe, Late Cretaceous, 85–66 Ma.

Stylasterina an order of branching, lacy cnidarians in the class Hydrozoa. Like the milleporines, they are colonies of soft-bodied polyps but differ from other hydrozoans in having calcareous parts that fossilize. The typical length of a branch is 2–3 inches. New Zealand, Asia, Australia, and United States; Late Cretaceous to Recent.

Stylemys a genus of small terrestrial tortoises in the family Testudinidae. It was the earliest-known land turtle in North America, up to 3 feet long, with forelimbs too weak for burrowing. North America, Europe, and Asia; late Eocene to Miocene.

Stylemys nebrascensis a species of North American tortoise in the family Testudinidae. It was about 2 feet long, with an unusually high-domed shell. Nebraska, late Eocene to early Oligocene.

Stylonuridae a family of eurypterids in the suborder Stylonurina and superfamily Stylonuroidea. Noted for elongated appendages, including strong walking legs, they ranged in size from small to large. Europe and United States, early Silurian to Early Devonian, 440–410 Ma.

Stylonurina a suborder of merostomatan arthropods in the order Eurypterida. Although the stylonurines were rare compared to the other suborder, the Eurypterina, they include some of the earliest eurypterids (see ***Brachyopterus***) as well as the latest, the Mycteropoidea, which became extinct in the end-Permian extinction. Cosmopolitan, Ordovician to Permian, 460–252 Ma.

Styracosaurus a genus of ceratopsid dinosaurs in the subfamily Centrosaurinae. Rhinoceros-sized, about 18 feet long and weighing more than 3 tons, it had large armor plates on the head, a robust nasal horn, and a large neck frill crested with very long spikes. Alberta and Montana, Late Cretaceous, 76–74 Ma.

Subulitidae a family of siphonate marine gastropod mollusks in the clade Caenogastropoda and superfamily Subulitoidea. They were generally awl-shaped, from 1 to 2 inches long. Global distribution, Ordovician to Carboniferous.

Suchomimus a monospecific genus of primitive, crocodile-like dinosaurs in the family Spinosauridae and subfamily Baryonychinae, closely related to *Baryonyx*. A striking example of convergent evolution in comparison with crocodiles, *S. tenerensis* was bipedal and had a long tail and strong forearms. Its long, flattened skull was very similar to that of a crocodile and was well-adapted to catching fish with very long frontal teeth. *Suchomimus* had 120 cone-shaped teeth and was 40 feet long and 10–12 feet high at the hip. North Africa, Early Cretaceous, 121–113 Ma.

Sulcus plural sulci. A shallow groove or furrow on the surface of some part of an organism's body. In brachiopods, a sulcus is a characteristic furrow in the pedicle valve, usually corresponding to a fold or ridge in the brachial valve. In vertebrates, it usually refers to a furrow separating parts of the brain.

Sundance Formation a mostly sandstone Middle Jurassic formation in western North America. Composed of mainly marine deposits laid down in the inland waterway called the Sundance Sea, it contains few but important fossils of the period.

Sume marcosi see **Luciferidae.**

Sunwaptan the final age of the Cambrian, covering the last 3 million years, notable for its diverse trilobite faunas.

Supersaurus a genus of very large sauropodomorph dinosaurs in the family Diplodocidae. On the basis of specimens from Colorado and Wyoming, which account for about 35% of the skeleton, its length is estimated at 110–112 feet and its weight at up to 40 tons. See also **Sauropoda**. United States and Portugal, Late Jurassic, 152–150 Ma.

Suskityrannus hazelae a proposed new species of small theropod dinosaurs in the superfamily Tyrannosauroidea. Known from two partially articulated specimens, it seems to have been similar to the much larger tyrannosaurs but only about 9 feet long and less than 100 pounds. New Mexico, United States; Early Cretaceous, 95–90 Ma.

Suture line of ammonoids, the pattern of indented lobes and saddles on the edge of a septum, often used in classification of genera.

Suuwassea emilieae a species of sauropod dinosaurs placed tentatively in the family Dicraeosauridae, known only from a partial skeleton found in 2000 in Montana. Relatively small for a sauropod, *Suuwassea* is estimated at 45–50 feet. It is the only dicraeosaurid from North America. United States, Late Jurassic.

Swanscombe Man three hominin skull fragments found at Swanscombe, England, anatomically similar to *Homo sapiens* with a cranial capacity of around 1300 cc, dated at about 450,000 years ago.

Swartpuntia a genus of Ediacaran organisms tentatively placed in the proposed phylum Petalonomae. Its multifoliate structure resembles *Pteridinium*, and it may be related to *Ernietta*. Between 5 and 8 inches long, its vertical petaloids extend from the length of a wide stem; there are at least three petaloids and probably more. Known best from several well-preserved specimens from the Nama Formation of Namibia, dated at 544–541 Ma, the very end of the Ediacaran. Namibia, United States, Australia, and Russia; late Ediacaran to early Cambrian.

Sycidiales an extinct order of charophytic algae in the class Charophyceae and division Charophyta. It is notable for its uncommon gyrogonites, which have porous vertical walls, as opposed to the characteristically spiral walls of later charophytes. The earliest-known species, *Sycidium siluricum*, is considered the earliest-known bisexual plant. Global distribution, Silurian to Early Carboniferous.

Sylvian sulcus the lateral sulcus of the human brain, a shallow furrow between three lobes. The most prominent human sulcus, it is deeper in most primate brains; it is a deep cleft in the most primitive monkeys.

Symbos cavifrons a species of North American woodland musk ox, an artiodactyl ruminant mammal in the family Bovidae. It is known from the early Pleistocene and was one of many large ruminants whose extinction at the end of the Pleistocene was probably human-related.

Symmetrodonts formerly considered an order of primitive mammals, but the term is now used in an informal sense to refer broadly to a large number of early mammaliamorphs close to the line of descent from cynodonts to mammals. The name refers to the symmetrical arrangement of the upper and lower molar teeth. See also ***Chronoperates, Kuehneotherium,*** and ***Morganucodon*****.** North America, Europe, and Asia; Late Triassic to Late Cretaceous or Paleocene.

Symphalangus the siamangs, a genus of the largest gibbons in the family Hylobatidae. Indonesia, Pleistocene to Recent.

Symphysops a genus of average-sized asaphid trilobites in the family Cyclopygidae. Like other cyclopygids, it had large compound holochroal eyes, but they were located to the side and under the vaulted glabella, which extended forward into a thorn. The name ("eyes growing together") refers to the visor-like, wrap-around eyes. *Symphysops* was pelagic and probably swam upside down. Europe, Asia, Africa, and North America; Middle to Late Ordovician.

Symphysurus a genus of asaphid trilobites in the family Nileidae. It was medium-sized, about 3 inches long. Global distribution, Early to Late Ordovician.

Synapomorphy an apomorphy shared by a group of lineages to the exclusion of other groups, indicative of monophyly and therefore a key to inferring evolutionary relationships by identifying common ancestors.

Synapsida a large group of advanced amniotes in the clade Reptiliomorpha, identified primarily by a lateral temporal fenestra in the skull behind each eye. Large and bulky, the synapsids ranged in length up to 20 feet; they had a heterodont dentition and were mostly carnivorous or insectivorous, with some herbivores. The synapsids diverged in the Late Carboniferous from the other main group of amniotes, the Sauropsida. They include the primitive group called pelycosaurian reptiles and the more advanced therapsids, the ancestors of mammals. The pelycosaurs, such as *Dimetrodon* and *Edaphosaurus*, were gradually displaced by the therapsids in the late Permian. The early synapsids all disappeared in the Triassic, with the only survivors into the Jurassic being the cynodonts and their descendants the mammals. Global distribution, Late Carboniferous to Recent.

Synapta an extant genus of very long sea cucumbers, holothuroid echinoderms in the order Apodida and family Synaptidae. Growing as long as 10 feet, *S. maculata* is now found in the Indian Ocean; its fossil record is sparse but may reach back as early as the Late Triassic. Cosmopolitan, Triassic to Recent.

Syndyoceras a genus of deerlike artiodactyl ungulates in the family Protoceratidae. About 5 feet long, it bore two pairs of horns, a V-shaped pair on a long snout and a pair curving inward above the eyes; its horns were slightly longer than the three pairs of *Protoceras*. United States, late Oligocene to early Miocene.

Synonyms two or more different names referring to the same taxon.

Syntrophiidina one of two suborders of impunctate articulate brachiopods in the order Pentamerida, more primitive than the second suborder, the Pentameridina. In addition to the pentamerid character of a short hinge line, the Syntrophiidina are characterized by an almost circular shell with a pronounced median dorsal fold. Global distribution, early Cambrian to Early Devonian.

Syntypes a set of several specimens that serve together as name bearers for a species if no holotype has been designated.

Synziphosurina a paraphyletic group of chelicerate arthropods in the extant class Xiphosura, related to the modern *Limulus.* They are characterized especially by free abdominal segments. Cosmopolitan, Ordovician to Devonian.

Syringophyllidae a family of tabulate corals in the extinct order Sarcinulida, with a horizontal and tubulate structure; global distribution, Ordovician and Silurian.

Syringopora a genus of tabulate corals in the order Auloporida and family Syringoporidae. Often called organ-pipe coral, *Syringopora* was phaceloid, with a sub-colonial structure of long, vertical corallites that were interconnected irregularly by horizontal tubuli. As the colony grew, it expanded horizontally, fanning out slightly toward the top. Global distribution, Ordovician to Permian.

Syringothyris a genus of articulate brachiopods in the superfamily Spiriferinida and family Syringothyrididae. Named for an internal tube around the pedicle valve, it had a punctate shell and a pyramidal shape. About 2 inches in diameter, it was semi-infaunal in lime substrates. Global distribution, Silurian to Permian.

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Tabula plural tabulae**;** a transverse septum between the walls of tabulate corals and some archaeocyathans.

Tabulata one of the two dominant Paleozoic corals, an order of wholly colonial cnidarians in the subclass Hexacorallia; see also **Rugosa**. The Tabulata are distinguished by tabulae within each of the corallites, which are almost always hexagonal; but see also **Vaughaniidae**. Appearing along with the rugose corals at the beginning of the Ordovician, they are especially characteristic of Silurian shallow seas. Declining after the middle Silurian and less common after the Devonian, they became extinct at the end of the Permian. Global distribution, Ordovician to Permian.

Tachypleus one of two surviving genera of horseshoe crabs, chelicerates in the order Xiphosurida and family Limulidae. See also ***Limulus***. China and Southeast Asia, Late Jurassic to Recent.

Taeniodonta a suborder of nonplacental eutherian mammals in the order Cimolesta. The taeniodonts varied greatly in size, from rat sized to bear sized (*Stylinodon*, of the Eocene). Some became highly specialized for digging, but efforts to categorize them on that basis are still tentative because of a sparse fossil record. Western North America, Late Cretaceous to Eocene.

Taeniolabidoidea a suborder of primitive mammals in the order Multituberculata. Although mostly small and rodent-like, some were the largest of the multituberculates. *Taeniolabis taoensis* weighed more than 200 pounds, similar in size to *Castoroides*, the largest beaver of the Pleistocene. North America and Asia, Late Cretaceous to early Eocene.

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Taeniopteris a genus of Mesozoic treelike plants in the Pentoxylales. Especially widespread from the Permian to the Jurassic, it had leaves as long as 16 inches. Global distribution, Carboniferous to Late Cretaceous.

Taimyr wolf a 35,000-year-old fossil of a wolf on the Taimyr Peninsula. According to a DNA analysis in 2015, it is a previously unknown species that indicates a date between 27,000 and 40,000 years ago for the splitting off of dogs from wolves, earlier than previous estimates. Siberia, late Pleistocene.

Tanis site see **Bowman site**.

Tanystropheus a genus of large archosauromorph reptiles in the extinct order Protorosauria and family Tanystropheidae. It is notable for a very long neck (10 feet) composed of only 13 elongated vertebrae, while its body and tail together were only about 10 feet long. It was probably a semiaquatic piscivore. Europe and Asia, Middle Triassic.

Tanytrachelos a genus of small amphibious reptiles in the extinct order Protorosauria and family Tanystropheidae. The type species *T. ahynis* is a long-necked archosauromorph only 1–2 feet long; it is known best from 200 specimens found in the Solite Quarry. United States, Late Triassic, 225–220 Ma.

Tapejaridae a family of pterodactyloid pterosaurs, probably related to the Azhdarchidae. The tapejarids had a large bony crest and had better vision than most pterosaurs. Many possessed a distinctive rounded crest, sometimes as wide as 3 feet. Global distribution, Early to Late Cretaceous.

Taphocoenosis a taphonomic association of fossils, either autochthonous or allochthonous. The term is sometimes used to refer specifically to an allochthonous assemblage of fossils transported after their death and deposited together, so that the assemblage does not represent a functional community in life. The term thanatocoenosis, on the other hand, refers specifically to an autochthonous death assemblage of organisms that died together.

Taphonomic artifact an artificial result of some accident during the process of fossilization. It is thus not indicative of the actual structural relationships of the parts of the organism.

Taphonomy the study of an organism's history between its death and the time of its discovery. Three taphonomic stages are recognized: necrosis (death), biostratinomy, and diagenesis. Biostratinomy refers to what happens to the organism between necrosis and burial, while diagenesis refers to what happens to it after burial, principally the process of mineralization by replacement or recrystallization. Taphonomy is especially concerned with transported allochthonous deposits and with biases

present in deposition and fossilization, such as scavenger activity, different rates of disintegration and decomposition, displacement of the fossil by soil movement, and dissolution or mineral replacement of bones.

Tapinocephalus atherstonei a species of large dinocephalian therapsids in the family Tapinocephalidae. Up to 10 feet long and 2 tons, *Tapinocephalus* was one of the largest animals of its time. Karoo Basin, South Africa, middle Permian, 265–259 Ma.

Tapiroidea an extant superfamily of perissodactyl mammals in the suborder Ceratomorpha. Probably related to the early Eocene *Homogalax* and *Hyracotherium*, the tapiroids spread throughout the northern continents and diversified slightly in the middle Eocene. Spreading globally in the Oligocene with little evolutionary change, the tapiroids became extinct in the northern land masses, persisting in some places to about 10,000 years ago. In addition to the extant family Tapiridae, there were two smaller families, the Helalestidae and the Deperetellidae, which became extinct in the Oligocene. Several species of the genus *Tapirus* are still extant elsewhere. See also ***Cambaytherium*** and ***Heptodon***.

Tapirus californicus one of several late species of tapiroids in the family Tapiridae. The species is known from New Mexico to Southern California in the early and middle Pleistocene. United States, Pleistocene.

Tapocyon a genus of primitive mammals in the family Miacidae. Coyote sized, it had retractable claws and was partly arboreal. Southwestern United States, Eocene.

Tarbosaurus bataar a species of large carnivorous dinosaurs in the subfamily Tyrannosaurinae. A close Asian relative of *Tyrannosaurus rex*, it was 33–39 feet long and weighed 5 tons or more. Although some consider it synonymous with *T. rex*, small skeletal differences of skull shape and the structure of jaw and digits seem to indicate simply a close relationship. Two elongated eggs discovered in 1993, purportedly of this species, are at 16.5 inches long the largest dinosaur eggs known. Northern China, Late Cretaceous.

Tardigrada The "water bears," an extant minor phylum of almost microscopic animals, called tardigrades because of their slow, lumbering gait. There are about 400 modern species, most of them living in water films on lichens and other plants, and some living on the bottom of ponds and ocean basins. They have eight legs, most of which are only 0.1 to 0.5 mm long. They are notable for their ability to survive long periods of cryptobiosis, complete dormancy; a large group in a European Space Agency experiment survived in a vacuum for a week in orbit around the Earth. The group does seem to have existed as long as most other modern phyla, although no fossils were known until their discovery in the 1990s in Cambrian deposits in Siberia. The only other known fossils are a few specimens in Cretaceous amber.

Tarsiidae an extant family of haplorhine primates in the infraorder Tarsiiformes. Tarsiers, now restricted to Southeast Asia, arose in the middle Eocene and became widespread in North America, Europe, and Asia, with two disputed African species from the Eocene and Oligocene (see ***Afrotarsius***).

Tarsophlebiidae a family of damselfly-like insects in the order Odonata. Probably stem-anisopterans, they are well-known from several exceptionally preserved specimens. They had two pairs of wings and long legs, with a wingspan and body length of 1–2 inches. Germany, England, and Kazakhstan; Late Jurassic to Early Cretaceous.

Tasmanian tiger see ***Thylacinus***.

Taxideinae the American badgers, a subfamily of caniform omnivores in the family Mustelidae, also spelled Taxidiinae. Appearing in central North America in the Miocene, the ancestors of the modern badger *Taxidea* spread across North America as far south as Mexico before disappearing at the beginning of the Pliocene, when they were replaced by *Taxidea*. North America, late Miocene to Recent.

Taxocrinida an order of articulate crinoid echinoderms in the extinct subclass Flexibilia. The Taxocrinida had a small, conical cup and crown, attached to the substrate by a stalk. Global distribution, Middle Ordovician to Permian.

Taxocrinus a genus of robust crinoids in the order Taxocrinida and family Taxocrinidae. It had a long, slender, circular stem and a 2 inch crown consisting of 5–10 robust basal arms. United States, Europe, China, and Australia; late Silurian to Late Mississippian.

Taxodioxylon a form genus of tree wood in the family Cupressaceae. The tree is estimated to have been 30–40 feet high. Europe, North America, and China; Late Jurassic to Paleocene and possibly Miocene.

Taxon a named group of organisms sharing unique features that differentiate the group from other taxa.

Taxonomy the study of the nomenclature and classification of organisms in groups according to their descent and evolutionary relationships.

Teichaster a genus of sea stars, asteroids in the order Valvatida and family Goniasteridae. With arms 4 inches long and a double row of large rectangular plates along the edge of the body surface, *Teichaster* was a robust sea star. Europe, Late Cretaceous to Miocene.

Teilhardina a genus of marmoset-like haplorhine primates tentatively placed in the family Omomyidae. It is probably polyphyletic, and its species are being reassessed. United States, Europe, and Asia; early to middle Eocene.

Teilhardina magnoliana a very small primate in the family Omomyidae. An arboreal primate, it is known from a single specimen discovered in Mississippi in 2008. The earliest-known primate in North America, it was mouse sized, weighing about an ounce, and resembled a small marmoset. United States, early Eocene.

Teinolophos trusleri a poorly known species of monotremes, placed tentatively in the family Steropodontidae. Probably the earliest relative of the platypus, *Teinolophos* is estimated at 4–5 inches long but is known only from four lower jaw fragments. See also **Steropodon**. Victoria, Australia, Early Cretaceous, 124–122 Ma.

Teleoceras a genus of perissodactyl mammals in the family Rhinoceratidae. Standing 9 feet high and weighing 1 ton, it resembled the hippopotamus except for a small nasal horn. North America and France, early Miocene to early Pliocene.

Teleocrater rhadinus a species of dinosauromorph archosaurian reptiles. From 7 to 10 feet long, *Teleocrater* had a thumb-sized depression in its hip socket bone at the location where dinosaurs had a hole in the socket enabling leg verticality rather than the splayed-out leg posture characteristic of reptiles. It also had a supratemporal fossa, a depression at the top of the skull. Both of these characters are considered defining features of dinosaurs, but increasing numbers of dinosauromorphs are now known to display various combinations of them. Tanzania, Middle Triassic, 247–242 Ma.

Teleosauridae a family of aquatic crocodylomorphs in the clade Thalattosuchia. They had elongate snouts and forelimbs only half as long as the hindlimbs, resembling the modern gharial. The Teleosauridae ranged in length from 6 to more than 16 feet, with some estimates much higher. North and South America, Europe, Africa, and possibly China; Early Jurassic to Early Cretaceous.

Teleostei an infraclass of actinopterygian fishes in the superclass Osteichthyes. The teleosts comprise 50 percent of all known vertebrate species and 96 percent of all extant species of fish. The earliest teleosts appeared in the Triassic; see, for example, ***Leptolepis*** and ***Pholidophorus***. Teleosts are characterized by moveable upper jaw bones, which allow the jaw to protrude forward; fully homocercal (symmetrical) tail fins; and thin, bony scales. Most teleosts reproduce by external fertilization of eggs, with generally no paternal care; a few genera are viviparous and somewhat altricial. Early Triassic to Recent.

Telephinidae a family of nektic trilobites in the order Proetida. See also ***Opipeuterella. G***lobal distribution, Early to Late Ordovician.

Telson the rearmost section of the body of many arthropods.

Temnospondyli "cut vertebra," a large, diverse, and long-lived order of semiaquatic and marine tetrapods, generally considered primitive amphibians. They include the first vertebrates to fully adapt to terrestrial life. Ranging in size from very large (*Mastodonsaurus*) to very small, they flourished in the late Paleozoic and the Triassic, and some genera survived into the Cretaceous. Some group of temnospondyls is considered likely to be ancestral to the Lissamphibia, the modern amphibians, but the relationships are disputed; see **Dissorophoidea**. Global distribution, Carboniferous to Cretaceous.

Tempskya a genus of Cretaceous ferns, the only genus in its family, Tempskyaceae. It grew to about 15 feet and appeared tree like, but its false trunk consisted of thin rhizomatous stems intertwined with small adventitious roots. Its leaves grew directly from the upper parts of the trunk, not on branches or in a crown. Global distribution but primarily Northern Hemisphere, Early to Late Cretaceous.

Tenrecidae an extant family of small afrotherian mammals in the superfamily Tenrecoidea. With the other afrotherians, they are related to hyraxes, elephants, and sirenians. They are known from Namibia since the Eocene and are now found in Madagascar and some parts of eastern and southern Africa.

Tentaculitida an enigmatic order of mollusk-like lophophorates, *incertae sedis*. Usually less than an inch long but up to 2 inches, their ribbed calcitic shell is straight and conical. See also **Coniconchia** and **Cornulitida**. Global distribution, abundant in some localities; Early Ordovician to Early Carboniferous.

Teratophoneus curriei a species of carnivorous tyrannosaurid dinosaurs known only from a partial skull and postcranial skeleton found in 2010 in the Kaiparowits Formation of Southern Utah. It is estimated at about 12 feet tall and 20 feet long. United States, Late Cretaceous, 76–74 Ma.

Teratornithidae a family of vulturelike birds that includes the largest-known flying birds, known principally from the Americas. The North American genera (at least four species in three genera identified so far) on average were about 40 percent larger than the modern condor. *Teratornis merriami*, the best-known teratorn because of many specimens recovered from the La Brea Tar Pits, had a wingspan of 12 feet but weighed only 30–35 pounds. The largest-known of the family is *Argentavis magnificens*, known from several partial specimens found in South America; it had a wingspan of 20–26 feet and may have weighed up to 170 pounds. (For the largest wingspan of a flying bird, see ***Pelagornis sandersi***.) Predators and

scavengers, the last of the teratorns became extinct about 10,000 years ago. North and South America, Miocene to late Pleistocene.

Terebratellidina a small extant suborder of articulate brachiopods in the class Rhynchonellata and order Terebratulida. They are characterized by a long loop, a punctate shell, and a median septum. Global distribution, Triassic to Recent.

Terebratulida an extant order of brachiopods in the class Rhynchonellata. The punctate shell is typically astrophic, oval or circular in outline, usually smooth, and there is often an aperture in the pedicle valve. The great bulk of living brachiopods are terebratulides. Global distribution, Silurian to Recent.

Terebratulidina an extant suborder of large articulate brachiopods in the class Rhynchonellata and order Terebratulida. They are characterized by a short loop, internal spicules, and a punctate and generally biconvex, egg-shaped shell. The widespread modern genus *Terebratula* grows as long as 4 inches. Global distribution, Late Devonian to Recent.

Terebridae "auger shell," an extant family of neoogastropod mollusks in the superfamily Conoidea. From 1 to 3 inches long, the terebrids are elongate and high spired, superficially resembling the Turritellidae. Among their differences are flattened whorls, an apertural notch, and a venomous barb with which to stun prey. Global distribution, Eocene to Recent.

Teredinidae the shipworms, a family of marine bivalve mollusks. They are wormlike except that they use two small shells at the anterior end of the body to bore through wood, living inside their tunnel. Known worldwide, they range from 2 inches to 3 feet long and are very destructive. They live worldwide but are less active in brackish water, such as the Baltic Sea. Early Jurassic to Recent.

Teredo the most common genus of shipworms, marine bivalve mollusks in the family Teredinidae; global distribution, Late Jurassic to Recent.

Ternifine man fossil bones found in Algeria in 1954 in a stratum about 700,000 years old. Originally named *Atlanthropus mauritanicus*, it was later recognized as an example of *Homo erectus*.

Terrane a large fragment of continental crust differing from the surrounding crustal material because it originated a considerable distance away and was accreted to the continent by tectonic forces.

Tertiary a discarded term formerly used to refer to the first part of the Cenozoic era, from the end-Cretaceous extinction to the end of the Pliocene. This period of time is now divided into Paleogene and Neogene (see **Geologic Time Scale**).

Teruelictis a genus of mustelid mammals placed tentatively in the subfamily Lutrinae. About 2 feet long, it was probably an otter but is thought to be nonaquatic. It is known from a skull and partial skeleton that do not show the typical aquatic features of otters. Spain, late Miocene, 10 Ma.

Tessarolax a genus of gastropod mollusks in the extant family Aporrhaidae. It is notable for thin, curving spines 1–3 inches long, growing from the edge of the lip. United States, Europe, Africa, and Madagascar; Cretaceous to Paleocene.

Test In echinoids, the external skeletal covering, composed of calcium carbonate. In foraminiferans, the internal walls and external covering, composed of either calcium carbonate or agglutinated grains of sediment.

Testudines the turtles, an extant order of mainly aquatic reptiles with a hard dorsal carapace above the rib cage and a hard ventral plastron attached to the rib cage. Whether their origin was terrestrial or marine is still debated. Although long thought to be anapsids, they are now generally considered diapsids. The order was once called Chelonii, and the term *chelonian* refers to turtles in general. The earliest turtles are usually placed in a slightly different order or clade; see, for example, ***Desmatochelys***, ***Kayentachelys***, ***Odontochelys***, ***Palaeochersis***, ***Pappochelys***, and ***Proganochelys***. See also **Cryptodira** and **Pleurodira**. Global distribution, Late Triassic to Recent.

Testudinidae the modern land tortoises, a family of cryptodire tortoises in the extant order Testudines and superfamily Testudinoidea; global distribution, Cretaceous to Recent.

Tetanurans a large clade of predatory dinosaurs (including tyrannosaurids, ornithomimids, and others) that are more closely related to modern birds than to the ceratosaurs.

Tethys Sea a chiefly tropical body of water to the east of Pangaea from the late Permian to the Miocene, with Laurasia to the north, Gondwana to the southwest, and the land masses that became China and Southeast Asia to the east. See also **paleogeography**.

Tethytheria a disputed clade of ungulate mammals variously considered to include the extant proboscideans, sirenians, and hyracoids, and the extinct desmostylians and embrithopods.

Tetraceratops an obscure genus of small synapsids represented by a single 4 inch skull found in Texas in 1908. Despite its four-horned name, *T. insignis* has six small horns on its face. Generally considered *incertae sedis*, it appears to be a transitional genus midway between pelycosaurs and therapsids, the ancestors of mammals. United States, early Permian.

Tetracorallia see **Rugosa**.

Tetragraptus an early genus of dichograptid graptolites in the order Graptoloidea. It was planktic, with four stipes, pendent or horizontal, and no bithecae. *Tetragraptus* is an important index fossil because of its many widely distributed species in the Early Ordovician.

Tetralophodon a genus of elephant-like proboscideans in the extinct family Gomphotheriidae. Named for its specialized four-cusped teeth, it was about 8 feet high, with four tusks and a trunk. Europe, Asia, and North America; middle Miocene to early Pliocene.

Tetrapoda a superclass of vertebrate animals that includes many living and extinct taxa. The earliest tetrapods appeared in the fossil record in the Late Devonian period, at about 370 Ma. Various environmental pressures — including intense competition among the many marine animals, the growing presence of terrestrial plants along the shorelines, and climatic changes — led some marine organisms to be attracted to habitats along shallow shorelines, evolving into species that could adapt to terrestrial habitats. Anatomical changes in some Middle Devonian rhipidistian fish such as *Eusthenopteron* gave rise to lobe-finned sarcopterygians such as *Tiktaalik*, some of which evolved in the Late Devonian into an amphibian lifestyle. Especially notable are the bones of the lobe fins, which correspond closely to the arm, wrist, and hand bones of later vertebrates. These bones are a homologous trait in all vertebrates descended from the lobefin fish, including humans and even snakes (considered tetrapods because they are descended from diapsids, which had four limbs like other vertebrates). The earliest tetrapods had as many as eight digits, but the later ones only five, a trait that has survived in their descendants. The only modern sarcopterygians are the coelacanths and lungfish. See also ***Acanthostega*****,** ***Greererpeton*****,** ***Ichthyostega*****,** ***Koilops*****,** ***Latimeria*****,** **Panderichthys,** ***Perittodus***, **Romer's gap**, ***Silvanerpeton*****,** ***Tiktaalik***, ***Tulerpeton***, and **Whatcheeriidae.**

Tetrarhynchia a genus of articulate brachiopods in the extant order Rhynchonellida. Nutlike and up to an inch wide, it was characterized by coarse ribs, an incurved beak, and a width slightly greater than the length. Europe, Asia, and South America; Early Jurassic, 190–180 Ma.

Teuthida a discarded term for a paraphyletic order of squids, mollusks in the subclass Coleoidea. It is now replaced by the two extant orders Myopsida and Oegopsida. Because of the paucity of their fossil record, squid are very poorly known, but fossil specimens are known from the Cretaceous.

Texas Red Beds a series of lower-Permian formations in Texas and Oklahoma. The region includes some of the most prolific sites for a range of Permian reptiles, sharks, stem tetrapods, temnospondyls, and other amphibians. United States, early Permian.

Thalassocnus a genus of aquatic xenarthran sloths in the family Megatheriidae. It is represented by several species living in the Neogene off the western coast of South America. Herbivorous and about the size of a human, it is one of the few tetrapods that have returned to the sea and then become extinct (see also ***Neovison*****).** The earlier species were probably semiaquatic and the later species fully aquatic. Peru and Chile, late Miocene to late Pliocene.

Thalattosauria "ocean lizard," an order of primitive marine reptiles, difficult to classify but generally considered archosauromorph diapsids. Growing as long as 13 feet, they had a broad body, flattened tail, and paddle-shaped limbs. North America, Europe, and Asia; Middle to Late Triassic.

Thalattosuchia "sea crocodile," a clade of marine crocodylomorphs consisting of the Metriorhynchidae and the Teleosauridae; cosmopolitan, Early Jurassic to Early Cretaceous.

Thamnasteria a genus of scleractinian stony corals in the family Thamnasteridae. The corallites of a colony are joined together by the strong septa, producing a depressed surface of *millefiori* appearance. Global distribution, Triassic to Eocene.

Thamnopora a genus of ramose tabulate corals in the family Pachyporidae; formerly considered a species of the genus *Favosites*. *Thamnopora* formed a treelike colony with branches about an inch thick. It flourished worldwide from the early Silurian through the Devonian, with some species persisting in Australia and Asia to the late Permian.

Thanatocoenosis see **taphocoenosis.**

Thaumaptilon an enigmatic organism of the Burgess Shale biota, possibly a cnidarian. It resembles a sea pen and may be the earliest pennatulacean, although some Ediacaran organisms may be even earlier pennatulaceans. Canada, middle Cambrian, 508 Ma.

Thecae cases, receptacles, or sheaths in various animals such as graptolites and echinoderms. Graptolite thecae are chitinous structures that often resemble the teeth of a saw blade, protruding from the stipes and housing the individual zooids that make up the colony. Thecal arrangement and structure are important elements of graptolite classification.

Thecideida an extant order of small brachiopods tentatively placed in the class Rhynchonellata, but their classification is disputed. Known since the Triassic, they are now the only extant tropical brachiopods. They typically are cemented to a hard substrate, often to the undersides of corals or in coral debris. Cosmopolitan, Triassic to Recent.

Thecodont "socket tooth," a term referring to a dentition of teeth fixed in sockets in the jawbone. The term Thecodontia was long used to refer to a paraphyletic group of early archosaurian reptiles that included the ancestors of dinosaurs, crocodilians, and pterosaurs, appearing in the Permian and diversifying widely in the Triassic. Thus used, the term is obsolete; see **Dinosauromorpha**.

Thecosmilia a genus of stony corals, colonial scleractinian corals in the extant suborder Faviina. The corallites are phacelo-dendroid and about half an inch in diameter. *Thecosmilia* was an important reef builder, especially in the Jurassic. Global distribution, Late Triassic to Cretaceous.

Thectardis avalonensis a species of triangular fossils known only from the Mistaken Point biota. It is *incertae sedis* but has been suggested as the earliest sponge. Probably cone shaped in life with the apex anchored to the substrate, it grew to 2.5 inches wide and 7 inches high. Canada, Ediacaran, 578–560 Ma.

Thelodonti a contentious group of jawless fish still considered a class by some but probably polyphyletic. From 6 to 10 inches long, the thelodonts resembled the heterostracans and anaspids but are characterized especially by their thelodont scales, which are tiny, oval dermal denticles with ridges, furrows, and spikes. Global distribution, Middle Ordovician to Late Devonian.

Thelodus a genus of thelodont agnathan fish in the family Coelolepidae. *Thelodus* had a broad, blunt head and thick, bony, pear-shaped scales covering its body. From 6 to 10 inches long, it had a low dorsal fin, an anal fin, and flap-like pectoral fins. Holarctic distribution, middle Silurian to Early Devonian, 428–409 Ma.

Theosodon a genus of litoptern mammals in the family Macraucheniidae. Similar in appearance to the modern guanaco, they were almost 7 feet long and weighed about 200 pounds. South America, early to middle Miocene.

Therapsida an order of synapsid reptiles that included the dominant terrestrial animals of the Permian. The therapsids, formerly called mammallike reptiles, represent a transitional phase between their reptile ancestors and the early mammals of the Triassic, which probably evolved from a theriodont group of therapsids called cynodonts. The earliest therapsid may be the still-controversial *Tetraceratops* of the early Permian, and other basal therapsids such as the Anomodontia, Biarmosuchia, and Dinocephalia appeared in the middle Permian. Developing from the sphenacodontid pelycosaurs, therapsids became the dominant predators, replacing the pelycosaurs in the middle Permian and diversifying globally in the late Permian. The main groups of therapsids that survived the end-Permian extinction were the therocephalians, dicynodonts, and cynodonts. Only a few groups, including the cynodonts and anomodont dicynodonts, persisted into the Jurassic, as the archosaurs gradually replaced most of the therapsids.

Theria the principal subclass of mammals, including the Metatheria (marsupials) and Eutheria (placentals) but excluding the Monotremata. The earliest-known therians (see ***Fruitafossor***, ***Juramaia*****,** and ***Montanalestes***) appeared in the Middle Jurassic, but there is some evidence of their existence in the Early Jurassic.

Theridomyoidea a superfamily of rodents possibly related to the sciuromorphs. Several short-lived species are biostratigraphically important. Europe and Africa, Eocene to Miocene.

Theriodontia a large group of advanced carnivorous therapsids in the direct line of descent to mammals. Named for their mammallike teeth, they include the therocephalians and gorgonopsians in the late Permian and then in the late Permian the more advanced cynodonts. Global distribution except Australia, middle Permian to Recent.

Theriognathus a genus of therapsids in the family Whaitsiidae; synonym *Whaitsia*. About 3 feet long with a long, narrow snout, it exhibits mixed reptile and mammal characteristics. Africa and Russia, late Permian.

Therizinosauria a diverse clade of feathered herbivorous theropod dinosaurs, related to the sharp-clawed, carnivorous raptors, also called segnosaurs. Species in the group varied in length from 3 to 33 feet and weighed up to 5 tons. They were basically bipedal, with claws as long as 3 feet on their robust forelimbs; unusually, on each pes, they had four forward-facing, fully developed claws. Numerous eggs have been found that indicate little if any care by parents. They are known mainly from China, and some have been found in Central Asia and Utah, as well as their recognizable tracks in Alaska. Early Jurassic to the end of the Cretaceous.

Therocephalia a group of carnivorous therapsids in the clade Eutheriodontia, related to cynodonts and gorgonopsians. They were 2–3 feet long, with an elongated skull and several mammalian traits. Europe, Africa, Asia, and Antarctica; Permian to Middle Triassic.

Theropithecus an extant genus of large monkeys in the family Cercopithecidae. Weighing from 25 to 40 pounds, three species are known from the Pliocene of East Africa.

Theropoda a very large group of dinosaurs that spanned a great range of types and sizes. Traditionally considered saurischians, they are now often thought of as a separate suborder (see **Ornithoscelida**). Although generally carnivorous and the principal terrestrial carnivores of the Jurassic and Cretaceous, even some basal lineages had varied diets, and several groups were herbivorous. They were among the earliest dinosaurs, dating back to 231 Ma, and their clade includes all modern birds. Among the largest theropod groups are the Allosauria, Ceratosauria, Coelurosauria

(including the Ornithomimosauria and Tyrannosauridae), Dromaeosauridae, and Therizinosauria. Global distribution, Late Triassic to the end of the Cretaceous.

Thescelosaurus "marvelous lizard," a parrot-beaked genus of bipedal ornithischian dinosaurs in the herbivorous family Thescelosauridae, usually classified as ornithopods. About 12 feet long, it appeared in North America at the very end of the Cretaceous. In a specimen found in 1993, the heart was preserved well enough that computer tomographic scans seemed to reveal a four-chambered heart and an aorta, which would have been significant because close to the evolutionarily advanced heart structure of birds and mammals, and more efficient than the three-chambered heart of snakes and crocodilians. A more thorough examination in 2011, however, disputed these interpretations, and most specialists now think that the "heart" is simply a concretion. The manus had five digits and the pedes four. Western North America, 70–66 Ma.

Thlipsuridae a family of podocopid ostracods in the superfamily Thlipsuroidea; North America and Europe, early Silurian to Late Devonian.

Thrinaxodon "trident tooth," a genus of early nonmammalian cynodont therapsids in the family Thrinaxodontidae. A fox-sized carnivore, *Thrinaxodon* exhibits traits that are transitional between early synapsids and the mammalian traits of advanced cynodonts. South Africa and Antarctica, Early Triassic, 250–245 Ma.

Thylacinus cynocephalus a species of carnivorous marsupials in the extant order Dasyuromorphia and extinct family Thylacinidae. One of the "Tasmanian tigers," superficially doglike but unrelated to the Canidae, it is a prime example of convergent evolution. It was the size of a large dog (6 feet long), with a long muzzle and striking posterior dorsal stripes. The family appeared in the Oligocene and became a top predator in Meganesia. By the time of European colonization, the thylacines were extinct everywhere except Tasmania. *Thylacinus cynocephalus* is the only species to survive into the twentieth century, evidently becoming extinct in the 1930s. Meganesia, early Pliocene to Recent.

Thylacoleo "pouch lion," a genus of Australian marsupials in the extant order Diprotodontia and extinct family Thylacoleonidae. Resembling a small lion, it weighed up to 350 pounds and was about 4 feet long. It was probably carnivorous, but ambivalent dentition has led to intense debate about its diet and habits. *Thylacoleo* became extinct between 45,000 and 40,000 years ago, shortly after the arrival of humans in the continent. Australia, late Pliocene to late Pleistocene.

Thylacosmilus a genus of South American metatherian carnivores in the order Sparassodonta. Not a felid, it was more closely related to marsupials than placentals. The leopard-sized *Thylacosmilus* was similar by convergent evolution to the coeval sabertooth felids of other continents, such as *Smilodon*, with 6 inch canines

and powerful jaws that were very similar to those of *Smilodon*. Argentina, late Miocene to Pliocene.

Thyreophora a clade of genasaurian ornithischian dinosaurs that includes the ankylosaurs, stegosaurs, and other herbivores. Global distribution, Early Jurassic to Late Cretaceous, 200 to 66 Ma.

Thysanura See **Archaeognatha** and **Zygentoma**.

Tianyulong confuciusi a species of ornithischian dinosaurs in the family Heterodontosauridae. Known only from a single specimen, it was only about 28 inches long but probably a juvenile. *Tianyulong* was bipedal and had tufts of fuzz that seem to be primitive feathers. China, Late Jurassic, 158 Ma.

Tianzhushania a genus of acritarchs tentatively placed in the family Halkieriidae but possibly a protist. It is circular and has features that could be nuclei of animal or bacterial cells, but its nature is still unclear. Known from India and the Doushantuo Formation in China, late Ediacaran.

Tiaojishan Formation a series of interspersed volcanic and sedimentary rocks in northeastern China, dated between 165 and 153 Ma. It is an important source of fossil fauna and flora in the Yanliao biota, with many specimens well preserved by volcanic eruptions. It is especially notable for the stem mammaliaforms *Agilodocodon*, *Castorocauda*, *Docofossor*, *Juramaia*, and *Rugosodon* and also the theropod dinosaurs *Caihong juji* and *Anchiornis huxleyi*. China, Late Jurassic.

Tiktaalik roseae a species of stegocephalians known from several skeletons found on Ellesmere Island. The predatory *Tiktaalik* is a significant link between earlier sarcopterygians and the first four-legged land animals. It was 6–8 feet long and possessed a suite of characters adapted to moving on land as well as in water, especially its strong shoulders, weight-bearing fins, and bendable wrists and neck. It lived in shallow coastal waters about 375 Ma**,** possibly making brief forays onto land. See also ***Ventastega*** and **Tetrapoda**. Canada, Late Devonian.

Tillodontia a suborder of eutherian mammals in the order Cimolesta, probably related to the pantodonts. They were quadrupedal, and the largest was about 3 feet long. They combine ungulate, rodent, and carnivore features, such as gnawing teeth and clawed feet. North America, Europe, and Asia; early Paleocene to late Eocene.

Timurlengia euotica a species of early tyrannosaurs intermediate between the first tyrannosaurids and the larger ones of the Late Cretaceous. Discovered in 2004 and described in 2016, *T. euotica* was still only horse sized but was similar in several ways to its large cousin *Tyrannosaurus rex*, notably in having similar brain and ear features (named "well-eared" because of long inner ear canals that indicate good

hearing ability). It is dated at 90 Ma, early in the Late Cretaceous and in the middle of a 20 million-year gap in tyrannosaurid fossils. Uzbekistan.

Tingamarra fauna see **Murgon Fossil Site**.

Titanis walleri a North American genus of large, flightless phorusrhacid birds in the order Cariamiformes, known only from the southern United States. Like the other Phorusrhacidae, it probably attacked smaller animals from ambush. Known from fragments but no skull, it is estimated to have been 8 feet tall and up to 350 pounds. Early Pliocene to early Pleistocene.

Titanites a genus of ammonoids in the order Ammonitida and family Dorsoplanitidae. Strongly ribbed, it is one of the larger ammonoids, the largest species reaching more than 4 feet in diameter. See also ***Parapuzosia***. England, Late Jurassic, 151–146 Ma.

Titanoides a genus of mainly herbivorous mammals in the order Cimolesta and suborder Pantodonta. About 3 feet long and 350 pounds, these were unusual herbivores in having large canine teeth and five-clawed feet. North America, late Paleocene.

Titanophoneus a genus of large carnivorous therapsids in the order Dinocephalia and family Anteosauridae. The type species, *T. potens*, was as much as 10 feet long, with the long, heavy snout and interlocking incisors typical of dinocephalians. Russia, middle Permian, 268–265 Ma.

Titanoptera an order of neopteran insects in the subclass Pterygota. Many are large, some species having wingspans up to 16 inches. Although related to grasshoppers, they could not jump. Europe and Asia, Early to Late Triassic.

Titanosauria a clade of large, herbivorous sauropod dinosaurs. Titanosaurs are distinguished by a long tail, a fairly long neck, spoonlike or peg-like teeth, and solid vertebrae. Among the principal representatives are the Longkosauria, the Saltasauridae, *Rapetosaurus*, *Argentinosaurus*, *Patagotitan*, and *Sauroposeidon*. The well-known *Argentinosaurus* has been considered the largest, but estimates of recent partial specimens of other Patagonian titanosaurs range up to 130 feet in length and 90 tons. A very large colonial nesting ground, Auca Mahuevo, has been found in Patagonia, consisting of hundreds of titanosaur nests containing an average of 25 eggs each. Other similar nesting grounds have been found in Madagascar, India, and Spain. Global distribution but principally in southern continents, Early to Late Cretaceous.

Titanotheriidae see **Brontotheriidae**.

Titanotylopus a genus of even-toed ungulates in the family Camelidae. The largest camelid known, it was about 13 feet high at the shoulder. North America, Miocene to Pleistocene.

Togocyamus a genus of late stem group clypeasteroids in the family Fibulariidae, considered the first true sand dollar. It was very small, less than a quarter inch long, biscuit-shaped with a pitted surface. West Africa, late Paleocene.

Tomarctus a genus of canids in the extinct subfamily Borophaginae, probably close to the ancestry of modern dogs. Up to 3 feet long and about 40 pounds, it had very powerful jaw muscles, indicating bone-crushing ability, a hallmark of scavengers. North America, early to middle Miocene.

Tommotian biota an assemblage of invertebrates of the early Cambrian, named for the area where they were first discovered in Siberia but probably occurring worldwide; there are a few entire skeletons, but the assemblage consists mainly of fragments known collectively as a "**small, shelly fauna**," *q.v.*; 535–520 Ma.

Tongtianlong limosus a species of maniraptoran theropod dinosaurs in the family Oviraptoridae. Known from a single partially articulated specimen, which died in a splayed-limb posture with its neck raised, was 7 feet long. Feathered and bipedal, it had a sharp beak and a dome-like skull roof with a low crest. Southern China, Late Cretaceous, 71–66 Ma.

Toothplate a specialized biting or crushing structure in the occlusal areas of the mouth of several types of fish, including placoderms and several genera of rays, lungfishes, and chimaeroids. Even some rhynchosaurian reptiles have a type of toothplate.

Tornieria africana see ***Barosaurus***.

Torosaurus a genus of ceratopsid dinosaurs in the subfamily Chasmosaurinae. *Torosaurus* had a skull 9 feet long and by two large fenestrae in its 5-foot-wide neck frill which provide its name. It had two large horns projecting forward above its eyes and other smaller horns behind its frill. The herbivorous *Torosaurus* weighed about 5 tons and was about 30 feet long. North America, Late Cretaceous, 68–66 Ma.

Torrejonia see ***Plesiolestes***.

Torvosaurus a genus of large carnivorous theropod dinosaurs in the family Megalosauridae. The largest species, *T. gurneyi*, weighed almost 5 tons and was about 33 feet long; known from several partial remains, it is the largest theropod known from Europe. A nest of *T. gurneyi* eggs found in Portugal contains the most primitive dinosaur embryos known. The other species, *T. tanneri*, is known from

remains found in Utah and Colorado in the United States. Late Jurassic, 153–146 Ma.

Toxasteridae a family of sea urchins, irregular atelostomate euechinoids in the order Spatangoida, with an elongated oval shape. Global distribution except Australia, Early to Late Cretaceous.

Toxodon platensis a South American ungulate, the type species of the family Toxodontidae. About 8 feet long and 5 feet high, *Toxodon* became extinct only about 11,000 years ago. Southern South America, Pliocene to late Pleistocene.

Toxodonta a suborder of mostly South American ungulates in the order Notoungulata. The toxodonts were between 4 and 10 feet long, the larger genera resembling a modern rhinoceros in appearance and size, but without a horn. Some species have nasal openings on the top of the skull. Research in 2014 suggests that the toxodonts may be related to the perissodactyls (odd-toed ungulates). South and North America, late Paleocene to late Pleistocene.

Toxodontidae a family of large notoungulates in the suborder Toxodonta. The family was principally South American but is known also from the Pleistocene in Central America and the southwestern United States; Oligocene to late Pleistocene.

Trace fossil see **paleoichnology** and **fossil.**

Trachodon a dubious genus of dinosaurs, identified from teeth and dental fragments, some of which are now known to be from a ceratopsid and some from a hadrosaur. See also ***Edmontosaurus***. North America, Late Cretaceous, 77 Ma.

Tragulidae an extant family of primitive hornless artiodactyls in the suborder Ruminantia. Commonly called chevrotains or mouse deer, they appeared in the Eocene, descended from the Hypertragulidae. Widespread in Eurasia in the Oligocene and Miocene, they are currently represented by three genera in Asia and Africa.

Transitional species a species that bears traits clearly indicating the sequential phases in the evolution of a new species, specifically traits common to both its ancestors and its descendants. See, for example, ***Amphistium*****, flatfish,** ***Heteronectes*****,** ***Samotherium***, ***Tetraceratops***, and **Theropoda**.

Traversodontidae a family of sheep-sized herbivorous therapsids in the suborder Cynodontia. They appeared in the Early Triassic, diversified widely throughout the period, and became extinct in the Early Jurassic. They are known mainly from South America and Southern Africa but have been found also in Madagascar, North America, Europe, and India; 242–200 Ma.

Tremarctinae a subfamily of short-faced bears, carnivorous mammals in the family Ursidae. Its extinct members include *Arctodus* and *Plionarctos*. The subfamily is still extant only in one species, *Tremarctos ornatus*, found in limited places in the Andes. South America, North America, and Europe; late Miocene to Recent.

Trematosauroidea a superfamily of labyrinthodont temnospondyls, amphibians in the suborder Stereospondyli. They were medium-sized fish eaters, some almost completely marine. The Trematosauroidea were one of only two or three groups of temnospondyls that survived the Triassic extinction. Global distribution, Early Triassic to Middle Jurassic.

Trepostomata an order of colonial bryozoans in the extant class Stenolaemata. They form treelike colonies, seldom preserved intact, the fragmented branches forming a major part of some Ordovician limestones. They are characterized by long, curving, impunctate, calcareous tubes, filled with closely spaced diaphragms. Global distribution, Ordovician to Triassic.

Treptichnus pedum a trace fossil that marks the GSSP for the beginning of the Cambrian Period and the Paleozoic Era. One of the earliest complex trace fossils, it is the burrow of an animal similar to modern priapulid worms. Newfoundland, Canada, 541 Ma.

Triadobatrachus a genus of frog-like amphibians in the suborder Proanura and family Triadobatrachidae. The only recognized proanuran, *Triadobatrachus* was 4 inches long and had 14 trunk vertebrae, a transitional feature since the typical amphibian had 24 and modern frogs only 4 to 9; it also had frog-like pelvic characteristics. Known only from one specimen found in Madagascar, Early Triassic, 250 Ma.

Triarthrus "three-jointed," a genus of ptychopariid trilobites in the family Olenidae, it was the last of its family. One of the few trilobites found with intact appendages, it was about 2 inches long and characterized by jointed, inward-facing spines on the legs and a smoothly rounded pygidium. Good examples are known from Beecher's Trilobite Bed in New York, especially notable for the spine details and for information about the protaspis and meraspis phases. Researchers in 2017 also reported the first known direct evidence of trilobite reproduction in a cluster of very small pyritized eggs near the head of a *Triarthrus* specimen from Beecher's. Global distribution, Early to Middle Ordovician, 488–446 Ma.

Triassaraneus andersonorum Selden a species of true spiders (Araneae) placed tentatively in the clade Araneomorphae, the first to be found in South Africa. Known from several specimens of varying completeness, it seems to be an early araneomorph. The best of these is an almost complete part and counterpart specimen from the Molteno Formation of South Africa. Late Triassic (Carnian), between 230 and 222 Ma.

Triassic the first period of the Mesozoic Era, from 252.2 to 201.3 Ma, divided into Early, Middle, and Late Epochs. After the end-Permian extinction, diversity was greatly reduced. On land, the archosaurs and the few remaining therapsids experienced a great radiation. The Triassic overall was a relatively hot and dry period, dominated by a great diversity of reptiles, especially the pseudosuchian archosaurs. Mammaliaforms and dinosauromorphs appeared in the middle of the period, and the pterosaurs — the first flying vertebrates — at the end of the Middle Triassic. At the end of period appeared the largest vertebrates known up to then, an increase culminating in the largest ever, the sauropod dinosaurs, but also including at least one elephant-sized non-dinosaurian, the dicynodont *Lisowicia*.

The great coal swamps of the late Paleozoic almost disappeared during the dry Triassic, but conifers, cycads, and corystosperms (see ***Dicroidium***) flourished throughout the period.

Sauropterygians and ichthyosaurs dominated the seas, and scleractinian corals appeared in the Middle Triassic, becoming important reef builders late in the period. Only one lineage of ammonoids survived the end-Permian extinction, but from it, the ceratitid ammonoids diversified rapidly and became very numerous throughout the Triassic. Evolving by the end of the Triassic were also the ammonitids, which were to become the dominant ammonoid group of the Jurassic and Cretaceous

Triassic extinction the fourth of the five great extinctions, at the end of the Triassic Period. It affected land and sea, causing the extinction of one class of marine animals, the conodonts, one-third of all marine genera, and many families of terrestrial animals. One-third of all known animal species of the Triassic did not survive, creating vacant ecological niches that the dinosaurs could occupy in the Jurassic. However, plant fossils and palynomorphs show no appreciable effects. As with all five mass extinctions, the causes are unclear; paleoclimatological research has found a marked increase in the level of carbon dioxide in the atmosphere near the end of the period, and other possible causes have been suggested. Some researchers have argued that at least two extinction pulses occurred. But the second, between 201.5 and 201.3 Ma at the end of the Rhaetian Age, is the one usually referred to as the Triassic extinction.

Triassochelys see ***Proganochelys***.

Tribrachidium heraldicum a unique species of soft-bodied, benthic trilobozoans. It was triradially symmetrical and is known only from negative impressions in overlying strata. *Tribrachidium* is limpet shaped, circular, and about an inch in diameter, but its upper surface is a shallow cone with three lobes in a triple-spiral triskelion pattern. Australia and Russia, Ediacaran, 558–555 Ma.

Triceratops "three-horned face," a genus of ceratopsid dinosaurs in the subfamily Chasmosaurinae. The largest weighed as much as 12 tons and were 26–28 feet long and 10 feet tall. The best known is the type species *T. horridus*; another species, *T. prorsus*, may have been the larger. *Triceratops* had a very large, 10 foot skull with a

parrotlike beak; a large, bony neck frill; and three horns. Herbivorous and eating a highly fibrous diet, it had replaceable grinding teeth. End-Maastrichtian specimens from the Hell Creek Formation show an interesting transition from small to larger nasal horn size, along with a transition from long to shorter beak size. Known only from the Late Cretaceous of North America, 68–66 Ma.

Trichopherophyton a genus of small, primitive vascular plants. Thought to be a zosterophyll, it is known only from the Rhynie Chert. Scotland, 410–405 Ma.

Triconodonta see **Eutriconodonta**.

Tridacna the largest bivalve, an extant genus of giant clams in the family Cardiidae. Ranging up to 750 pounds and 4 feet wide, *Tridacna* has very deep folds on the margin and is found typically in shallow coral reefs. Worldwide in the tropics, Miocene to Recent.

Trigoniidae an extant family of articulate bivalve mollusks in the order Trigoniida. They are large and roughly triangular, with striking patterns of ribbing and a very complex articulation and elaborate hinge teeth. Although trigoniids were widespread in the Jurassic and Cretaceous, they were thought to have become extinct at the end of the Cretaceous until a living member of the family (now named *Neotrigonia*) was discovered in 1802 in Australia. Global distribution, Late Carboniferous to Pliocene.

Trigonodidae a family of bivalves in the order Trigoniida. Its four genera were disaster taxa, appearing in the Permian, flourishing globally in the Early Triassic, and disappearing by the Early Jurassic.

Trigonostylopidae a family of South American hoofed mammals in the order **Astrapotheria**, *q.v.*

Trigonotarbida a large group of primitive arthropods in the order Arachnida, superficially resembling spiders. They were probably predators on other arthropods, and some Devonian genera developed armor, spines, and tubercles. They did not have spinnerets and probably did not produce venom. Trigonotarbids are well-known, especially from the European Coal Measures of the Late Carboniferous. Europe and North and South America, early Silurian to early Permian.

Trilobita a very large class of mostly small marine arthropods. The earliest definitive arthropods (see also ***Spriggina*** and ***Parvancorina***), the trilobites had a hard exoskeleton made of chitin reinforced with calcite; a longitudinally three-lobed body, for which they are named; and a series of biramous limbs. The body is also divided in three parts from the head (cephalon) to thorax to tail (pygidium), generally also having a post-segmental telson. They are sometimes found enrolled, curled into a ball. Although trilobites averaged less than an inch in length, a few species

grew as long as 28 inches (see ***Isotelus rex***). They were mostly benthic and often burrowed in the top layers of sediment, but some small species were evidently planktic. They used a great variety of feeding strategies: detritus-feeding, filter-feeding, grazing, scavenging, and predation.

Trilobites arose in the Precambrian. Estimates of their origin range as early as 700 Ma, but the earliest-known fossil specimens are dated between 530 and 521 Ma; see ***Callavia***, ***Profallotaspis***, and ***Nevadia***. They were among the earliest animals to develop complex eyes; some were blind, but most had compound eyes (see **holochroal** and **schizochroal**). Trilobites underwent a massive radiation in the late Cambrian; more than 6,000 species from the Cambrian have been described. Since the hard exoskeleton fossilized relatively easily, trilobites are among the most abundant fossils of the Paleozoic. Their abundance and their worldwide distribution make them stratigraphically important, especially through the middle of the Paleozoic. After flourishing in the Ordovician and Silurian, they began to decline in the Devonian, and the only group to survive the Devonian extinctions was the large order Proetida. The proetids flourished through the Carboniferous, dwindling in numbers thereafter up to their extinction at the end of the Permian. Early Cambrian to Permian.

Trilobitomorpha a subphylum of arthropods comprising only the class Trilobita.

Trilobozoan a term for a group of disk-shaped Ediacaran fossils that display triradial symmetry. Some consider them cnidarians, and others group them as a separate phylum. The best known are *Tribrachidium*, *Anfesta*, and *Albumares*. Australia, Russia, and Canada; late Ediacaran, 570–540 Ma.

Trimerellida an order of inarticulate brachiopods in the class Craniforma. Besides the superfamily Trimerelloidea, it contains only a few other genera, such as *Adensu* and *Ussunia*, the latter being considered intermediate between the Trimerellida and the extant Craniida (see **Craniiformea**). The Trimerellida had a thick shell, and the pedicle is sometimes attached to another brachiopod. The representative genus *Trimerella* includes important Late Ordovician index species. Global distribution, Early Ordovician to late Silurian.

Trimerocephalus a genus of eyeless trilobites in the order Phacopida and family Phacopidae. It is noted for a specimen of a single-file line of individuals in close physical contact with each other, evidently dying suddenly while migrating. Europe, Asia, and Australia; restricted to the Famennian Age of the Late Devonian, 371–365 Ma.

Trimerophytopsida an extinct class of early vascular plants in the division Tracheophyta; synonyms Psilophytopsida, Trimerophytales, and Trimerophyta. Arising in the Early Devonian from the rhyniophytes, the trimerophytes are generally considered ancestral to the progymnosperms and ferns and so to almost all higher plant life today. Global distribution, Devonian to Carboniferous.

Trimerus a genus of phacopid trilobites in the family Homalonotidae and related to the calymenids. *Trimerus* is distinguished by a wide, shovel-shaped cephalon and small, raised eyes. Global distribution, Silurian to Devonian.

Trinil fauna a biostratigraphic faunal assemblage in eastern Java that contains the remains of *Homo erectus* commonly referred to as "Java Man." See also **Ngandong** and **Jetis**. Indonesia, late Pleistocene.

Trinucleidae a family of small, blind trilobites in the order Asaphida and superfamily Trinucleoidea, important as index fossils in the Ordovician. They are characterized by an almost circular shape up to an inch across, long genal spines, a vaulted glabella, and a ribbed and pitted border around the large cephalon, which accounts for about half of the body length. The trinucleids became extinct in the Ashgill event, 444 Ma, at the end of the Ordovician. The type genus is *Trinucleus*, but see also ***Cryptolithus***. Global distribution, Middle to Late Ordovician.

Trinucleoidea a superfamily of trilobites in the order Asaphida. Very diverse and widespread through the Ordovician, they declined toward the end of period. The only family that survived into the Silurian was the Raphiophoridae. Global distribution, late Cambrian to middle Silurian.

Trionychidae a large extant clade of softshell cryptodire turtles in the order Testudines. Global distribution, Late Cretaceous to Recent.

Trionyx an extant genus of soft-shell freshwater turtles in the subfamily Trionychinae. It is a cryptodire, up to 3 feet long, with a long, narrow head. Global distribution, Early Cretaceous to Recent.

Triops cancriformis an extant species of tadpole shrimp, notostraca branchiopods in the family Triopsidae. From 2 to 4 inches long and resembling a small *Limulus*, it is known from the Grès à Voltzia Lagerstätte and remains almost unchanged today. Europe, Triassic to Recent.

Triopsidae an extant family of tadpole shrimp, the single family of phyllopod branchiopods in the order Notostraca (but see also **Kazacharthra**). From 1 to 4 inches long with a broad, flattened carapace, its two genera (*Triops* and *Lepidurus*) are little changed since the Carboniferous. Global distribution, Early Carboniferous to Recent.

Tritheledontidae a family of small advanced cynodont therapsids; formerly called **Ictidosauria.** Mainly insectivorous, the largest species being less than 10 inches long, they were probably replaced in the Jurassic by early mammals. South America and Africa, Late Triassic to Middle Jurassic.

Tritylodontidae a family of mammaliamorph therapsids in the clade Cynodontia. Tritylodonts were generally herbivorous, with protruding incisors and three rows of grinding cheek teeth. They had a prominent sagittal crest and are estimated to have been about 2 feet long. Global distribution, Late Triassic to Early Cretaceous, 220–110 Ma.

Trochanter a rough prominence at the proximal end of the femur in many vertebrates. A fourth trochanter and an associated depression in the bone is one of the identifying traits for dinosaurs.

Trochiliscales an early order of charophytic algae characterized by dextrally coiled gyrogonites; cosmopolitan, Silurian to Carboniferous.

Trochoid in snails and some rugose corals, shaped like a toy top.

Troodon a genus of small, agile theropod dinosaurs in the family Troodontidae, related to the pachycephalosaurus. Up to 8 feet long and 150 pounds, it is notable for evidence of birdlike nesting and egg-laying behavior, including possible brooding behavior by males. Although its diet is uncertain, *Troodon* was probably primarily carnivorous and predatory; it is notable for unusual serrated teeth. It also has a sickle claw on each pes and a partly opposable digit on each manus. China, Russia, and North America, found recently even in northern Alaska; Late Cretaceous, 78–76 Ma.

Trucherognathidae "ragged jaw," a family of fibrous conodonts. They are characterized by fibrous, platelike teeth resting in a depression on the jaw ramus rather than grasping the ramus or the jaw tip. North America, Europe, and Asia; Middle Ordovician.

Tryblidium a genus of large monoplacophorans in the order Tryblidiida. From 1 to 2 inches long, it had a pear-shaped shell, in some species composed of an outer calcitic and an inner aragonitic layer. North America and Europe, Ordovician to Silurian.

Trypanites an ichnogenus of trace fossils, unbranched cylindrical borings made by marine worms, narrow and generally straight or slightly curving. *Trypanites* is one of the most common trace fossils, occurring in rocks, hardground, and shells.

Tsidiiyazhi abini a species of sparrow-sized birds in the extant family Coliidae (the mousebirds), described in 2017 as the earliest-known tree-dwelling bird. Found in New Mexico, it is dated at 62.5 Ma and is evidence of a rapid speciation in birds following the end-Cretaceous extinction. United States, early Paleocene.

Tuatara see **Sphenodon.**

Tubuliporata see **Cyclostomatida**.

Tubuliporina still extant, the largest suborder of bryozoans in the order Cyclostomatida. Variable in form, the tubuliporines attach to hard substrates, either encrusting or standing erect. Global distribution, Late Triassic to Recent.

Tuditanomorpha a suborder of microsaurian lepospondyl tetrapods. They are identified by several skeletal features, especially a common basic pattern of skull bones. North America and Europe, Early Pennsylvanian to late Permian.

Tulerpeton curtum a species of early tetrapods in the order Ichthyostegalia, closely related to *Acanthostega* and *Ichthyostega*. One of the few well-known labyrinthodonts from the period of time called Romer's gap, *Tulerpeton* lacked gills and had six digits on each limb. Russia, Late Devonian, 365–361 Ma.

Tulites a genus of ammonitid ammonoids in the family Tulitidae. Involute and finely ribbed, several species are important stratigraphically in the Lower and Middle Bathonian. Europe and Saudi Arabia; Middle Jurassic, 168–164 Ma.

Tullimonstrum gregarium the famous "Tully monster," a soft-bodied chordate in the class Hyperoartia. Possibly a stem lamprey, it is known only from the Mazon Creek site southwest of Chicago. From 6 to 8 inches long, it had stalked eyes and a notochord. United States, Late Pennsylvanian.

Tunicata a large extant subphylum of basal marine chordates; synonym Urochordata. Tunicates have a notochord only in their free swimming larval phase; as adults, they are benthic and sessile. The main group is the Ascidiacea, commonly called sea squirts. Global distribution, Cambrian to Recent.

Tuojiangosaurus a monospecific genus of ornithischian dinosaurs in the family Stegosauridae. Similar to the better-known *Stegosaurus*, *T. multispinus* was 24 feet long and weighed about 3 tons. It is notable for 17 pairs of spikes and plates along its backbone. China, Late Jurassic, 161–155 Ma.

Turkana Boy the name given to a nearly complete hominin skeleton found in 1984 near Lake Turkana, tentatively assigned to *H. ergaster*. It is the most complete early hominin skeleton known. Kenya, 1.6 Ma.

Turrilites an unusual genus of ammonoids in the order Ammonitida, suborder Ancyloceratina, and family Turrilitidae. Its helical, auger-like shell is high spired and tightly coiled, with a strongly ribbed surface. Global distribution, Late Cretaceous, 100–90 Ma.

Turritellidae "tower shell," an extant family of caenogastropod mollusks in the superfamily Cerithioidea. From 1 to 4 inches long, the elongate, filter-feeding turritellids are very high spired, with ornamentation on their many convex whorls, and an operculum which can be withdrawn inside the shell. Global distribution, Triassic to Recent.

Turtle Graveyard a locality in Slope County, North Dakota, that has produced many turtle fossils from the time of the end-Cretaceous extinction, especially baenids. With six taxa of turtles, including partial skeletons of plastomenids and other still-extant trionychids, it may be the oldest and most diverse turtle thanatocoenosis known. United States, Late Cretaceous to early Paleocene.

Turtles see **Testudines.**

Tutusius umlambo a species of Devonian tetrapods that lived inside the Antarctic Circle. Described in 2018, *Tutusius* is known from a single shoulder bone and is estimated at about 3 feet long. See also ***Umzantsia***. South Africa, Late Devonian.

Tuzoia a genus of bivalved organisms tentatively classified as stem arthropods. Probably nektobenthic, it had a pair of large stalked eyes and a circular carapace from 6 to 8 inches in diameter. North America, Europe, Asia, and Australia; early to middle Cambrian.

Two Medicine Formation an important geologic formation of the Campanian, encompassing a large area of northwestern Montana and southern Alberta. Laid down along the western shore of the Western Interior Seaway between 84 and 71 Ma, the Two Medicine strata contain fossils of numerous Late Cretaceous dinosaurs as well as many other terrestrial and freshwater animals. North America, Late Cretaceous.

Tylocidaris a genus of sea urchins, echinoids in the order Cidaroida and family Psychocidaridae. Like *Pseudocidaris*, it is notable for club-shaped spines, narrow at the proximal end and bulbous at the distal end. Europe and North America; Early Cretaceous to late Eocene.

Tylopoda "swollen foot," an extant suborder of artiodactyl ungulates, originating in North America in the middle Eocene and found only there until the early Pliocene. Although once placed in the Ruminantia, they are not true ruminants. The modern representatives are the Camelidae, the camels and camelids of Asia and South America.

Tylosaurus proriger a large species of mosasaurs in the subfamily Tylosaurinae. The type species of the genus, *T. proriger,* was almost 50 feet long and weighed up to 11 tons. Distinguished by an elongated, cylindrical snout, it inhabited the shallow

Western Interior Seaway of North America in the Late Cretaceous, with a diet including fish, shellfish, and small aquatic birds. Although most *Tylosaurus* specimens have been found in North America, they are known also from Spain, New Zealand, and Antarctica; 85–70 Ma.

Type species as defined by the ICZN, the name-bearing type of a genus or subspecies. A type species is considered the typical representative of a genus with which the name is permanently taxonomically associated. A type genus has the same relationship to a family.

Type specimen see **holotype**.

Typostrophism a saltationist theory of evolution espoused by the German paleontologist Otto Schindewolf in the middle of the twentieth century. Schindewolf stressed catastrophically destructive events as the principal cause of mass extinctions and of the subsequent emergence of new taxa, relegating natural selection to a secondary role in evolution. See also **Unspecialized Descent**.

Typotheria a probably paraphyletic suborder of South American ungulates in the extinct order Notoungulata, possibly including the hegetotheres. Ranging from rabbitlike to bear sized, the typotheres shared several characters with rodents. The Interatheriidae and Mesotheriidae are the largest of the five families in the suborder. Late Paleocene to middle Pleistocene.

Tyrannosauridae a family of large predatory dinosaurs in the superfamily Tyrannosauroidea. Similar in many ways to the earlier allosaurs (which had died out by 92 Ma), the Tyrannosauridae became the dominant predators in their ecosystems toward the end of the Cretaceous. Widespread in North America and eastern Asia, Late Cretaceous, 81–66 Ma.

Tyrannosauroidea a superfamily of theropod saurischian dinosaurs. Arising in the Middle Jurassic, the early tyrannosauroids were relatively small up to the middle of the Cretaceous; see, for example, ***Guanlong***, ***Eotyrannus***, and ***Moros***. They were bipedal but had well-developed forelimbs with three digits, while the later tyrannosaurs, which became the largest terrestrial predators known, had relatively weak forelimbs and two digits. Known mainly from Laurasia but also found in South America and Australia. Global distribution, 165 to 66 Ma.

Tyrannosaurus rex the type species of the family Tyrannosauridae, *T. rex* reached lengths up to 45 feet and 12–15 feet high at the hips; estimates of its weight vary from 7 to 18 tons.

Like the more recently discovered *Albertosaurus*, a close relative, *T. rex*, was among the most powerful predators in the history of life. Its massive skull was more than 3 feet long, with several dozen serrated teeth up to 6 inches long. It had broad

skull attachments for its powerful jaw muscles and very large vertebrae that supported its massive head. Bipedal, with very strong hindlimbs, it had relatively weak forelimbs only 3 feet long; each manus had two claws. Although the teeth did not meet, coprolites indicate that *T. rex* may have chewed and crushed even the bones of small prey by a shearing action of its teeth. Like other large predators, *T. rex* was probably also a scavenger, but it was fast enough and strong enough to capture prey on its own.

Tyrannosaurus rex is noteworthy for an unusual pattern of holes in its skull that may indicate a more advanced nervous system than most other dinosaurs, and it may have had stereoscopic color vision, although nothing is known of its visual acuity. Its life span has been estimated at 27–30 years, and its normal walking speed was about 5 miles an hour, but it probably reached speeds as high as 18 miles an hour. The first partial skeletons of *T. rex* were found in Montana by Barnum Brown in 1900 and 1902, and about a dozen partial skeletons have been found since in South Dakota, Wyoming, Montana, and Alberta. One of the most complete skeletons, referred to as "Sue," is now on display in the Field Museum in Chicago. North America, Late Cretaceous, 68–66 Ma.

Tyrannotitan chubutensis a species of large theropod dinosaurs in the family Carcharodontosauridae. Known from a partial skeleton found in Patagonia, it had long, grooved, sharklike teeth and was 35–40 feet long. Closely related to *Giganotosaurus* and *Mapusaurus*, it is one of the oldest Carcharodontosaurus known. Argentina, Early Cretaceous, 121–112 Ma.

U

Ugrunaaluk kuukpikensis a dubious species of hadrosaurs in the subfamily Saurolophinae. It is so similar to *Edmontosaurus* that some researchers consider them the same species. A duck-billed dinosaur that lived above the Arctic Circle near the end of the Cretaceous, *Ugrunaaluk*, bore crests along its spine and is estimated at 25 to 30 feet long and 7 feet high at the hip. Several thousand bones belonging to the species have been found on the Colville River in northern Alaska in strata from 69 Ma. Late Cretaceous.

Uintacrinida a small order of stemless crinoids that includes only two genera, ***Marsupites*** (*q.v.*) and *Uintacrinus*; global distribution, Late Cretaceous, 87–84 Ma.

Uinta Mountains the highest mountains of Utah and an important source of fossils from the Precambrian Eon to the early Cenozoic, uplifted by the Laramide orogeny. The Uinta Mountain Group at the core is dated as far back as 1,000 Ma, and its uppermost strata contain Ediacaran acritarchs and other Neoproterozoic fossils. These are overlain by the Cambrian Lodore Formation, containing rare trilobites and brachiopods. At succeeding higher elevations are found fossils from almost all Paleozoic periods, followed by a great variety of fossils from the Mesozoic. Here the Upper Jurassic Morrison Formation and the Upper Cretaceous Mancos Shale have produced especially a great quantity of dinosaur fossils.

Uintatheriidae a family of large, primitive herbivorous mammals in the order Dinocerata. The subfamily Uintatheriinae was widespread in North America in the early Eocene, being replaced in its large-browser niche in the middle Eocene by the brontotheres. The last of the family was *Gobiatherium*, known in Mongolia up to the late Eocene. The United States and Mongolia, late Paleocene to late Eocene.

Uintatherium a genus of large browsing mammals in the order Dinocerata; the type genus of the family Uintatheriidae. Up to 12 feet long and weighing as much as 2 tons, *Uintatherium* resembled the modern rhinoceros in shape but was not

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related. Its skull was very thick and bore six frontal ossicones. The United States and China, middle to late Eocene.

Uloboridae a family of araneomorph spiders in the superfamily Deinopoidea. Venomless, they entrap their prey in cribellate silk and enclose it, generally in an irregularly shaped shroud. Although they are known worldwide, from as early as 165 Ma, their fossil record is very sparse. Cosmopolitan, Middle Jurassic to Recent.

Umm Irna Formation a series of alluvial strata in Jordan that were laid down in an equatorial environment at the boundary of the Permian and Triassic periods, between 252 and 250 Ma. The site is important especially for the flora, containing specimens of several typically Mesozoic plants such as corystosperms, podocarps, and Bennettitales, along with a typical Permian *Glossopteris* flora.

Umoonasaurus a monospecific genus of Early Cretaceous plesiosaurs in the family Leptocleididae. *Umoonasaurus demoscyllus* was about 8 feet long and had three crest-like ridges on the skull. It swam in a shallow sea of Central Australia about 115 Ma.

Umzantsia amazana a species of early tetrapods that lived inside the Antarctic Circle near the end of the Devonian. Described in 2018 along with *Tutusius*, another tetrapod from the same location, *Umzantsia* is known from several disarticulated bones, principally a lower jaw. Its length is estimated at about 28 inches. Living close to paleolatitude 70 degrees south, it existed in a much cooler environment than other known tetrapods of the time. Waterloo Farm, South Africa, Late Devonian, about 370 Ma.

Ungulates a general term for the many typically herbivorous mammals whose digits are capped with hooves instead of ending in nails or claws. Late Cretaceous to Recent.

Uniformitarianism Until the eighteenth century, the accepted view was that life on Earth has been affected throughout its history by sudden catastrophic events—such as great floods, widespread volcanic eruptions, and rapid formation of mountain chains—which led to the more or less universal destruction of all life forms but which no longer occur. In the period after such catastrophes, new and basically different life forms were thought to have appeared to repopulate the devastated regions.

As knowledge of the fossil record increased in the eighteenth and nineteenth centuries, this view became untenable, and the theory of uniformitarianism gained credibility, advanced especially by James Hutton and Charles Lyell. Uniformitarianism stressed the idea that changes in the past were gradual and were caused by essentially the same forces of change observable in the present. From about 1850 to 1950, this view developed into the modern synthesis, becoming

almost universally accepted in the middle of the twentieth century, with gradualism considered a hallmark of evolutionary change. In the succeeding decades, a more complex view has emerged, giving more importance to occasional catastrophic events that cause relatively rapid changes in the conditions of life. Research in regulatory genes has also led some to assign greater importance to macromutations in evolution. See also **punctuated equilibrium** and **typostrophism**.

Unionida an extant order of freshwater bivalves, including the freshwater pearl mussels. Most species in the order are parasitic in the larval stage, attaching to the gills or fins of fish. Cosmopolitan, Triassic to Recent.

Uniramia "one branch," a term sometimes used for a grouping of arthropods including myriapods, onychophorans, and hexapods (insects).

Unspecialized Descent, Law of Also called Law of the Unspecialized, it was formulated by E.D. Cope. It holds that the typical taxa of any temporal unit are not closely related to the most highly developed and specialized taxa of the previous epoch but are rather descended from the least specialized taxa. Otto Schindewolf made it an important part of his anti-Darwinian theory of typostrophism, summarizing it thus: "Evolution builds upon that which has remained simple." Although the concept contains an obvious general truth, its use in typostrophism has been widely refuted as oversimplified.

Uptonia jamesoni a species of ammonitid ammonoids in the family Polymorphitidae, an important index fossil in the Pliensbachian. It was evolute, strongly ribbed, and about 4 inches high. Europe and Greenland, Early Jurassic, 191–184 Ma.

Uraraneida an order of arachnids in the subclass Tetrapulmonata. As its name indicates, the order contains the earliest proto-spiders, including *Attercopus fimbriunguis* and *Permarachne novokshonovi*. Still poorly known, the uraraneids lack developed spinnerets, retain a segmented abdomen, and have a flagellum resembling that of scorpions. The United States and Russia, Middle Devonian to Permian.

Urasterella a genus of small sea stars in the order Platyasterida. Unusual for a sea star, *Urasterella* has only a minute central disc, giving it the appearance of a brittle star. It has long, slender arms covered with small, irregular plates, but they extend to only 2–3 inches wide. North America and Europe, Middle Ordovician to middle Silurian.

Urochordata see **Tunicata**.

Urodela the salamanders, an order of tailed amphibians, synonym Caudata. Identified by a slender body, a blunt snout, and a permeable skin, many species are fully aquatic and others fully terrestrial. They have no scales or claws and generally

live in cooler regions and moist environments. The urodelans probably branched off from the lobe-finned fish in the Devonian or Early Carboniferous, but the earliest fossils are known from the Jurassic (see ***Karaurus*** and ***Kokartus***). Global distribution, Jurassic to Recent.

Ursidae the bears, an extant family of mammals in the clade Caniformia and superfamily Arctoidea. The ursids evolved from canids such as *Cephalogale* in the Miocene and are now found on all continents but Antarctica.

Ursus spelaeus the cave bear, a species of omnivorous mammals in the family Ursidae. About the size of the largest modern bears and differing only in a few characters, it became extinct between 24,000 and 10,000 years ago. Europe and Asia, Pleistocene.

Utahraptor a genus of theropod dinosaurs in the subfamily Dromaeosaurinae, known from several specimens found in eastern Utah. Estimated at up to 23 feet long and half a ton, it is probably the largest-known dromaeosaur, and it seems to be of a heavier build than its cousins *Deinonychus* and *Velociraptor*. Like other dromaeosaurs, it hunted in packs. The United States, Early Cretaceous, 130–125 Ma.

V

Vaceletia an extant monospecific genus of sphinctozoan sponges. The sphinctozoans were thought to be extinct since the Cretaceous until *V. crypta* was discovered off the northeastern coast of Australia in 1977. Important because of a rich Mesozoic fossil record, *Vaceletia* may be related to the ceractinomorph demosponges. Global distribution, Cambrian to Recent.

Vagaceratops **a monospecific genus of ceratopsian dinosaurs in the subfamily Chasmosaurinae. Known from three skulls found in southern Alberta, it is very similar to the coeval *Kosmoceratops*, which is known only from southern Utah. Both have a striking neck frill, square-topped in *Vagaceratops* but fringed by many hornlets, some curving forward. It was 15–20 feet long and had only a short nose horn. Canada, Late Cretaceous, 75 Ma.**

Valenictus chulavistensis an extinct species of walrus in the extant family Odobenidae and subfamily Odobeninae. Found in Southern California, it had tusks only slightly shorter than those of the modern walrus *Odobenus*, and it is very similar to *Odobenus* except that it had no teeth besides the tusks. See also ***Dusignathus*****.** California, Pleistocene, 3 Ma.

Varanops a genus of primitive synapsid reptiles in the family Varanopidae. About 4 feet long, it is a larger version of its cousin *Varanosaurus*. Both are known only from the Texas Red Beds of Texas and Oklahoma. The United States, early Permian, about 280 Ma.

Varanosaurus a genus of pelycosaurian synapsid reptiles in the family Ophiacodontidae. From 3 to 5 feet long, it had a long snout adapted for grasping prey, with a set of sharp teeth including two pairs of longer teeth at the tip of the snout. Texas, United States, early Permian, 280 Ma.

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Varanus priscus a species of very large monitor lizards in the family Varanidae; synonym *Megalania*. Ancestral to the modern Komodo dragon, it is estimated at 18–23 feet long, and it may have weighed about a ton. Australia, Asia, Europe, and Africa; early to late Pleistocene.

Variscan orogeny a late-Paleozoic mountain-building process, caused by tectonic shifting; also called Hercynian orogeny. It is associated with the convergence of Laurasia and Gondwana in the Devonian and Carboniferous to form Pangaea. See also **paleogeography**.

Varves finely layered seasonal deposits of sediment in freshwater lakes, often distinguishable as summer and winter layers. Since varves represent such a brief time of deposit, they are especially useful in assessing past changes in climate.

Vaughaniidae a family of tabulate corals in the superfamily Favositicae. It is characterized especially by shallow, rounded corallites and the absence of tabulae. The type species is *Vaughania cleistoporoides* Garwood. Europe, Early Carboniferous.

Vegavis iaai a species of duck-like birds in the suborder Anatoidea, known from only one specimen but generally considered the first anseriform bird. About 1 foot long, it is the earliest-known waterfowl. CT scans indicate that it had a voice box and could probably vocalize as modern birds do. *Vegavis* was found on Vega Island in Antarctica and named for the Instituto Antártico Argentino, which described the first of two specimens in 2005. Late Cretaceous, 68–66 Ma.

Velociraptor a Mongolian genus of turkey-sized carnivorous dinosaurs in the family Dromaeosauridae. About 6 feet long but weighing less than 35 pounds, it was a bipedal feathered predator, marked by a large, forward-pointing claw on the top of each pes. This sickle claw may have been used for attack, as was probably true of *Utahraptor* and *Achillobator*, larger dromaeosaurs up to 20 feet long. Disagreement continues as to whether the claw was sharp enough to rip skin open or may have been used in tree climbing to a perch to pounce on prey. Mongolia, Late Cretaceous, 75–71 Ma.

Vendian see **Ediacaran**.

Ventarura lyonii a genus of small, primitive vascular plants, tentatively considered as zosterophyll. It was similar to and somewhat larger than *Trichopherophyton* of the nearby Rhynie chert. Known only from the Windyfield chert, Scotland; Early Devonian, 410–405 Ma.

Ventastega curonica a species of early stegocephalian tetrapods. From about 365 Ma, it is similar to *Tiktaalik*, another early tetrapod that was terrestrial as well

as aquatic. About 3 feet long, relatively large for the time, it is one of the earliest tetrapods yet found. Latvia, Late Devonian.

Ventral situated on or near the lower or anterior surface of an animal.

Ventriculites a genus of cup- or vase-shaped sponges in the class Hexactinellida. It is characterized by siliceous spicules fused into an irregular, rigid, perforated skeleton. Cosmopolitan, Jurassic to Eocene.

Verbeekinidae a family of highly specialized foraminiferans in the superfamily Fusulinoidea. They are distinguished generally by planispirally coiled tests. Global distribution, early to late Permian.

Vernanimalcula guizhouena a monospecific genus of microscopic acritarchs that display some bilateral symmetry. Found in the Ediacaran Doushantuo Formation of China, it is dated at between 600 and 580 Ma, 40 million years before the earliest undisputed bilaterians. It was first described as a bilaterian, but the claim has been widely disputed, so that even the kingdom in which *Vernanimalcula* should be placed is in doubt.

Vertebrata the subphylum of chordate animals that have a vertebral column containing a spinal cord, including jawed vertebrates and jawless, bony, and cartilaginous fish. There are about 66,000 species of vertebrates, accounting for 5% of all described animals. All vertebrates have an internal skeleton, a central nervous system running dorsally the length of the body, and gills or gill arches. (In mammals the jaw, the thyroid, the larynx, and the ossicles of the ear all correspond to the gill arches of earlier vertebrates.) For the earliest vertebrates, see ***Myllokunmingia***, ***Haikouichthys***, and ***Zhongjianichthys.***

Vertigo a genus of pulmonate gastropod mollusks in the family Pupillidae. It is a small land snail with a bulbous shell, smooth whorls, and a small aperture. Europe, Asia, and North America; Oligocene to Recent.

Vertisol a clay soil that is subject to extreme shrinking and expanding with environmental changes. Vertisols are taphonomically important in evaluating the burial position of fossils.

Verulam Formation see **Bobcaygeon Formation**.

Vestigial structures body parts of organisms that seem to have no function, such as hip bones of snakes and rudimentary hind limbs of whales. Such structures are to be expected in the process of natural selection and are among the more obvious evidences of evolution. See also **analogous** and **homologous structures.**

Veterupristisaurus a genus of theropod dinosaurs in the family Carcharodontosauridae. Described in 2011 as the oldest carcharodontosaurid and estimated to have been about 30 feet long, it is known from spinal fragments found in an Upper Jurassic formation dated at around 150 Ma. Tanzania, Late Jurassic.

Vetigastropoda an order of gastropod mollusks that includes the Pleurotomarioidea, Trochoidea, and several other groups of high-spired, turreted, and highly ornamented sea snails. Global distribution, late Silurian to Recent.

Vetulicolia an enigmatic subphylum of early to middle Cambrian organisms, tentatively considered deuterostomes. Their size ranges from microscopic to 4 inches long. They are generally elongate, with two segmented sections: a larger anterior section that contains several gill-like openings and a posterior tail-like section. They have no eyes or appendages but do seem to have a notochord and are considered chordates. See also ***Banffia*** and ***Saccorhytus***. Cosmopolitan, early to middle Cambrian.

Vibrissae whiskers, the long, stiff, thick hairs on the snout of many animals that are used as organs of touch. They are typical of mammals but are also known in some fish and birds and are suspected in some pterosaurs and dinosaurs. The vibrissae of pinnipeds are especially sensitive. In addition to these snout whiskers, called mystacial vibrissae, some mammals, especially rodents, also have supraorbital vibrissae above the eyes. The probability of mammalian vibrissae has been demonstrated in early prozostrodonts and demonstrated in early primates.

Vilevolodon diplomylos a species of early haramiyidan protomammals in the family Eleutherodontidae, notable for transitional features. About 3–4 inches long, it seems to have been a glider similar to the coeval *Maiopatagium*. It had fur and was warm-blooded, and its complex tooth crown dentition resembles that of modern squirrels; in other ways it was more reptilian than true mammals. China, Late Jurassic, 160 Ma.

Vintana sertichi a species of groundhog-like mammals in the family Sudamericidae. It is known from one specimen, discovered in Upper Cretaceous strata on the western coast of Madagascar. Weighing about 20 pounds, *Vintana* was much larger than other mammals of the time and is notable for well-developed olfactory bulbs in the brain. The almost intact skull increases what is known of the Gondwanatheria, early mammals known generally only from teeth and fragments of bone from the Late Cretaceous through the Miocene. Madagascar, Late Cretaceous, 72–66 Ma.

Viverravidae a family of early mammals in the extinct superfamily Miacoidea, related to early carnivores but believed to be unrelated to any modern carnivorans. They had an elongated skull with only two molars in the upper and lower jaws. North America, Europe, Asia, and Africa; early Paleocene to late Eocene.

Viverridae an extant family of omnivorous small mammals in the order Carnivora and suborder Feliformia. Although primitive, they have several living representatives, such as civets, genets, linsangs, binturongs, and perhaps mongooses. Global distribution, late Eocene to Recent.

Viviparidae a family of large freshwater gastropod mollusks in the superfamily Viviparoidea, called river snails. Their shells are subglobular and low-spired, with indented sutures and a large aperture with an operculum. Global distribution, Jurassic to Recent.

Volaticotherium antiquum a species of insectivorous eutriconodont mammals in the proposed subfamily Alticonodontinae. The earliest-known gliding mammal, it was about the size of a squirrel and had a patagium, but it is not related to the modern flying squirrel. Mongolia, Middle Jurassic, about 164 Ma.

Volborthella a problematic genus of early Cambrian fossils, once suggested as a cephalopod but now simply *Incertae sedis*. Its fragmentary siliceous specimens are widespread in North America, Greenland, and Europe in lower Cambrian strata, appearing earlier than trilobites and then concurrently with them through the early Cambrian. See also ***Salterella***.

Volchovia a poorly known genus of ophiocistioid echinoderms in the family Volchoviidae. Its turtle-like shell was high in the middle and flattened out toward the edges, like an inverted shallow vase. Russia, Ordovician to Silurian.

Voltzia a genus of early conifers in the family Voltziales, abundant in the Triassic Grès à Voltzia Lagerstätte, to which it gave its name. It was generally low-growing and bushy. Global distribution; Carboniferous to Triassic.

Voltziales an order of early coniferous trees in the class Pinopsida. The best-known genus is ***Walchia***, *q.v.* Global distribution, Carboniferous to Triassic.

Voluta a genus of marine gastropod mollusks in the superfamily Muricoidea and family Volutidae. About 4 inches long, the shell of *Voluta* is generally moderately spired, with sharply ribbed whorls and a narrow aperture. Global distribution, Cretaceous to Recent.

Vombatidae an extant family of Australian marsupials in the order Diprotodontia. The family diverged from other diprotodonts earlier than the late Oligocene, possibly in the late Eocene. Several genera of large Vombatidae became extinct in the late Pleistocene; see ***Phascolonus***. Australia, Oligocene to Recent.

Vorombe titan one of the elephant birds of Madagascar, a species of giant ratite birds in the order Aepyornithiformes and family Aepyornithidae; formerly named *Aepyornis titan*. It was about 10 feet tall and weighed more than 1000 pounds, probably the heaviest known bird. It is known only from Holocene dates in Madagascar and *became* extinct after humans arrived on the island.

Voulte-sur-Rhône see **La Voulte-sur-Rhône.**

Vulcanodontidae a proposed family of sauropodomorph dinosaurs, variously thought to include *Vulcanodon*, *Barapasaurus*, *Tazoudasaurus*, *Kotasaurus*, and *Gongxianosaurus*; some researchers include even *Isanosaurus* and *Antetonitrus* from the Late Triassic. Africa, Europe, and India; Late Triassic to Early Jurassic.

W

Wahweap Formation a rock formation in southern Utah, known mainly for several dinosaur specimens, especially *Lythronax argestes*. The United States, Upper Cretaceous, 84–72 Ma.

Waimanu a genus of flightless sphenisciform diving birds, considered a basal penguin. From 2 to 3 feet long, it is known in one confirmed species. New Zealand, middle Paleocene, 60–58 Ma.

Wakaleo a genus of carnivorous Australian marsupials in the extant order Diprotodontia and extinct family Thylacoleonidae. About 2.5 feet long, *Wakaleo* probably preyed on small animals. Australia, early to middle Miocene.

Walchia a genus of early conifers in the family Voltziales. It is especially important in tracking changes in the climate in the Pennsylvanian and early Permian. North America, Europe, and Asia; Late Carboniferous to early Permian, 310–290 Ma.

Walcott, Charles D. American paleontologist who discovered and investigated the **Burgess Shale** site, *q.v.*

Wallace's Line the imaginary line between the different fauna characteristic of Southeast Asia on one hand and of the islands closer to Australia on the other. The line, named for Alfred Russel Wallace, runs between parts of Indonesia, specifically through the Lombok Strait between Bali and Lombok, eastward between Borneo and Sulawesi, and then eastward south of Mindanao. The deepwater barrier represented by the line is thought to have existed for 50 million years, since the early Eocene. With few exceptions, both mammals and birds have remained separate on the two sides, even though the distance is quite small in places, especially in periods of great ice formation in the polar regions. In addition to terrestrial fauna, only one family of freshwater fish is found on both sides of the line (see **Osteoglossidae**).

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Walruses see ***Valenictus***.

Waptia a genus of shrimplike arthropods known primarily from *W. fieldensis* of the Burgess Shale. An earlier species is known also from the Chengjiang biota. About 3 inches long, *Waptia* had a thin exoskeleton and long antennae. China and Canada, early to middle Cambrian.

Wattieza see ***Eospermatopteris***.

Weichselia a genus of ferns in the extant order Gleicheniales and family Matoniaceae. Characterized especially by lobed leaves on 3-foot-long fronds, it spread rhizomatously, forming dense swards over large areas. Global distribution, Jurassic to Late Cretaceous.

Weigeltisauridae a family of gliding reptiles of the late Permian, now considered to include only two species of *Coelurosauravus* (previously named *Daedalosaurus*, *Glacialisaurus*, and *Weigeltisaurus*). About a foot long with a long tail, they had membranous winglike structures behind each forelimb, stretched on rodlike dermal bones. Europe and Madagascar, Lopingian, 260–251 Ma.

Wenlock Series a geological formation of Northern Europe, best known for a middle Silurian site in Western England that contains an important biota. The fossils occur inside carbonaceous nodules, best studied so far by a complex process involving digital photographs (see **Herefordshire Nodules**). The biota occurs in fine-grained deposits of volcanic ash interwoven with successive strata of carbonate mud. Organisms represented include polychaete worms, sponges, graptolites, microscopic radiolarians, and other uncommonly fossilized organisms. Northern Europe, Wenlock Epoch of the Silurian, 433–427 Ma.

Western Interior Seaway a shallow sea covering much of Central North America in the Cretaceous. In its largest phase, it was 600 miles wide, stretched from the Arctic Ocean to the Gulf of Mexico, and was connected by the Hudson Seaway across Eastern Canada to the Atlantic Ocean. Also called North American Seaway, Niobrara Sea, and Cretaceous Seaway. Early Cretaceous to early Paleocene.

Whaitsia see ***Theriognathus***.

Whatcheeriidae a small family of amphibians, stem-tetrapods from Romer's Gap. The family is named for What Cheer, Iowa, where a large deposit of fossils, including especially some early amphibians, was found in the 1990s. About 3 feet long, the type species *Whatcheeria deltae* is dated to 340 Ma, about the same date as *Greererpeton*. The family also includes *Pederpes finneyi* and possibly the Australian *Ossinodus*. The United States, Europe, and Australia. Early Carboniferous, 345–336 Ma.

Wheeler Shale a Konzentrat-Lagerstätte in the House Range of western Utah, dated at 507 Ma. Known principally for large numbers of trilobites (see ***Elrathia***), it has also produced specimens of *Anomalocaris*, *Wiwaxia*, and other early organisms such as bivalved crustacean arthropods, chancelloriids, vetulicolians, and priapulid worms (see ***Selkirkia***). The fauna is considered comparable to that of the coeval Burgess Shale. The United States, middle Cambrian.

Whippomorpha see **Cetancodonta.**

White River Group a large set of lower Oligocene deposits centered on southwestern South Dakota. The volcaniclastic strata have produced many articulated skeletons of mammals from the period of transition from subtropical forests to grassland, including entelodonts, oreodonts (*Merycoidodon)*, all three of the rhinocerotoids (see **Amynodontidae**, **Hyracodontidae**, and **Rhinocerotidae**), horses, hyaenodonts, canids, and some of the last of the brontotheres. The United States, late Eocene to early Oligocene.

Wielandiella a genus of bennettitalean shrubs or small trees in the family Williamsoniaceae. It had clusters of narrow leaves on slender branches. Europe and Asia, Late Triassic to Middle Jurassic.

Williamsonia a genus of small trees in the family Williamsoniaceae. Related to cycads, it is known worldwide from cones and fernlike leaves. Global distribution, including Antarctica; Late Triassic to Late Cretaceous.

Williamsoniaceae a family of spermatophyte trees in the order Bennettitales. Their reproductive processes are enigmatic, but they were related to cycads and similar in overall appearance to palms, some growing as high as 33 feet. Global distribution, Triassic to Cretaceous.

Windyfield chert a locality of Lower Devonian deposits similar to the Rhynie biota, located half a mile from the Rhynie site. Scotland, Lower Devonian, 410–405 Ma.

Winneshiek site a Middle Ordovician Lagerstätte in a meteorite crater in Iowa. Discovered in 2005, the site has produced significant eurypterids (see ***Pentecopterus***), conodonts, phyllocarids (see **Ceratiocarididae**), and other indeterminate fossils. The United States, Middle Ordovician, 470–460 Ma.

Wiwaxia a small, sluglike but armored animal of the middle Cambrian. First found in the Burgess Shale group and identified by Walcott as a polychaete worm, it is now tentatively classified as a mollusk, possibly a stem-polyplacophoran. It resembled a miniature sea urchin except that it had only two rows of spikes on its head and eight rows of carbonaceous sclerites covering its body, similar to those of an isopod.

Isolated specimens have been found elsewhere in North America and in Asia, Europe, and Australia, all dated between 513 and 505 Ma.

Worthenia a genus of marine gastropod mollusks in the family Lophospiridae. It was turban-shaped and about 2 inches high, and its whorls have a raised edge with fine ornamentation. Global distribution, Devonian to Jurassic.

Wukongopteridae a small family of pterosaurs represented by the genera *Darwinopterus* and *Wukongopterus* (the latter poorly known). The family is considered an example of modular evolution, having a long tail and other characteristics of the earliest pterosaurs, combined with the skull features of the more advanced pterodactyloids. China and England, Middle to Late Jurassic, 165–153 Ma.

Wynyardiidae a small extinct family of marsupials in the extant order Diprotodontia. Similar to the phalangerids, the opossum-like Wynyardiidae are intermediate between the primitive polyprotodont marsupials and the advanced diprotodonts. Australia, Oligocene to Miocene.

X

Xenacanthida

an order of late Paleozoic freshwater sharks in the superorder Euselachii; formerly called Pleuracanthodii. Eellike and as long as 13 feet, the Xenacanthida are distinguished by two-pronged teeth and a large serrated spine extending backward from the rear of the braincase. They appeared in the Carboniferous and spread worldwide in the Permian, but only a few genera survived the Permian extinctions before disappearing in the Middle Triassic.

Xenarthra

a clade of unusual placental mammals of the Americas that includes the living sloths, anteaters, and armadillos, as well as many extinct ancestors, including the glyptodonts, pampatheres, and ground sloths. Insectivorous or herbivorous, they were formerly referred to as paratheres or as edentates because of the lack of enamel on their teeth. Many genera are marked by varying degrees of body armor in the form of dermal ossicles. They are not related to the anteaters of Africa and Asia (such as the aardvarks, echidnas, numbats, and pangolins), both groups having evolved convergently to fill the same ecological niches. North and South America, late Paleocene to Recent.

Xenodiscus

a genus of ammonoids in the order Ceratitida and superfamily Xenodiscoidea. It was evolute and thinly discoidal, 2–4 inches high. Asia, North America, and Madagascar; middle Permian to Early Triassic.

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Xenopithecus

a proposed genus known only from a disputed jaw fragment, possibly of an early hominoid ape; Kenya, late Oligocene, 28 Ma.

Xenorophius

a genus of stem-odontocete whales in the family Xenorophidae, known from several partial specimens; southeastern United States, late Oligocene.

Xenungulata

an obscure order of large South American ungulates placed in the extinct superorder Meridiungulata. The order currently contains one family, the Carodniidae, with three genera. The group is still *incertae sedis* because of its inconclusive similarities to several other very different and widespread mammalian groups (such as the primitive Pantodonta, the Uintatheriidae of the Eocene, and the Embrithopoda). Argentina, Brazil, Colombia, and Peru; Paleocene to Eocene.

Xenusion auerswaldae

a species of basal onychophorans or lobopods in the class Xenusia. It is known only from two fragmentary specimens found in glacial debris. See also **Onychophora**. Northern Europe, early Cambrian.

Xiaotingia zhengi

a species of theropod dinosaurs placed tentatively in the family Anchiornithidae. Known from an articulated skeleton and skull, it was feathered and about the size of a chicken. China, Late Jurassic, 155 Ma.

Xinicaulis lignescens

a species of early palm-like trees, considered a cladoxylopsid. Although known only from sections of the trunk, it was probably 30–40 feet high and up to 3 feet at the base, with a crown of leaves at the top. China, Late Devonian.

Xiongguanlong baimoensis

a species of theropod dinosaurs in the superfamily Tyrannosauroidea. It seems to be an intermediate ancestor of the large tyrannosaurs of the Late Cretaceous. Although earlier fossils of much smaller ancestors of tyrannosaurs are known from England and China, *Xiongguanlong* is an important mid-weight relative. It possessed some of the characteristic features that made *Tyrannosaurus rex* such an

effective predator, such as broader skull attachments for massive jaw muscles, and thicker vertebrae to support a larger head. Southern Gobi Desert, China, Early Cretaceous, 110 Ma.

Xiphactinus

"sword-ray," a genus of large predatory actinopterygian fish in the family Ichthyodectidae. Between 15 and 20 feet long, it had a large gape and four large fangs at the tip of its snout for grasping prey. A 13-foot specimen at the Sternberg Museum in Hays, Kansas, is famous for having a well-preserved 6-foot ichthyodectid fish (*Gillicus*) inside its stomach. Global distribution, Early to Late Cretaceous.

Xiphodontidae

an extinct family of artiodactyl ungulates in the suborder Tylopoda. Known from several locations in Europe, the xiphodonts were generally slender and camel-like. Since the early evolution of the camel family is restricted to North America, they probably evolved separately, but a paucity of intermediate specimens makes their relationship unclear. The type genus *Xiphodon* is well-known in the late Eocene, and *Paraxiphodon* from the Eocene to the early Oligocene.

Xiphosurida

an extant order of marine chelicerate arthropods in the class Xiphosura. The order includes several Paleozoic families and is represented today by *Limulus* and *Tachypleus*, the horseshoe crabs; see also ***Lunataspis***. Global distribution, Late Ordovician to Recent.

Xylotitan

a genus of artiodactyl mammals in the family Brontotheriidae. This dwarf brontothere is the most abundant mammal in the Clarno Nut Beds of Oregon. United States, middle Eocene, 44 Ma.

Y

Yabeinosaurus tenuis a species of unusual reptiles in the order Squamata. It was relatively primitive compared to the other lizard lineages of its time but is considered a basal lizard, probably related to the early Iguania or Gekkota. *Yabeinosaurus* was one of many viviparous lizards; one specimen was preserved with 15 embryos, close to birth, in her body. It is known from several well-preserved juvenile and adult specimens, the largest about 1.5 feet long. China, Early Cretaceous, 125–122 Ma.

Ya Ha Tinda a Konservat-Lagerstatten in Alberta, first described in 2017. Located in the Lower Jurassic Fernie Formation, the site has produced well-preserved articulated marine vertebrates, mollusks, crinoids, crustaceans, and some plant fossils. Like the Holzmaden and Strawberry Bank sites of Europe, it is dated at 183 Ma, near the boundary of the Pliensbachian and Toarcian Ages of the Early Jurassic. Significantly, its fauna is remarkably similar to those of the European sites. Canada, Early Jurassic.

Yalkaparidon a problematic genus of marsupial mammals with possibly two species in their own order, Yalkaparidontia. Known only from one skull and isolated teeth found in the Riversleigh deposits, *Yalkaparidon* was a small animal, possibly mole-like. Australia, Oligocene to Miocene.

Yangchuanosaurus a genus of large theropod dinosaurs in the superfamily Allosauroidea and family Metriacanthosauridae. Known from several skulls and partial skeletons which have been described as at least two species, it was as long as 35 feet and very similar to *Allosaurus*. Heavily built, it had a long, massive tail and a skull 3.5 feet long, with a bony ridge on its snout. The largest predator in its environment, it preyed on sauropods and stegosaurs. China, Late Jurassic, 160–162 Ma.

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Yanliao biota an extensive assemblage of fauna and flora, also known as the Daohugou biota. Located in Liaoning, principally in the Tiaojishan Formation, it includes mainly stem-group taxa from the boundary between Middle and Late Jurassic. China, Middle to Late Jurassic, 168–159 Ma.

Yanoconodon a monospecific genus of small early eutriconodont mammals in the family Jeholodentidae. About 5 inches long, *Y. allini* is especially notable for its well-preserved ear bones, which represent a late stage in the evolution of the first mammals. It also had the unusual feature of lumbar ribs. Its date is uncertain but between 130 and 122 Ma. China, Early Cretaceous.

Yawunik kootenayi a species of Cambrian arthropods found in 2014 at the Marble Canyon site of the Burgess Shale. It had an external skeleton, segmented body, and jointed appendages. *Yawunik* could move its frontal appendages backward and forward when swimming and evidently caught prey in the toothed claws on some appendages. Canada, middle Cambrian, 508 Ma.

Yinlong downsi a species of early ceratopsian dinosaurs in the family Chaoyangsauridae. Known from several partial specimens, *Yinlong* is currently the earliest ceratopsian. About 4 feet long and 30–35 pounds, it had no horns and only a very small frill. China, Late Jurassic, 160 Ma.

Yinotheria a proposed basal subclass of mammals to include several Mesozoic stem-monotreme families and the still-living monotremes, the platypus, and four species of echidnas. They are known mainly from the Southern Hemisphere, with the exception of the Shuotheriidae, which are known from England and China. Late Triassic to Recent.

Yi qi see **Scansoriopterygidae**.

Yixian Formation a Lower Cretaceous (Barremian to early Aptian) formation in Liaoning, underlying the equally important Jiufotang Formation. Fossils from the Yixian Formation compose the larger part of the Jehol biota. Despite uncertainty about its age, the formation is thought to be between 125 and 121 Ma. China, Early Cretaceous.

Ymeria denticulata a genus of tetrapods possibly related to *Ichthyostega*, known from a partial skull, lower jaw, and a shoulder impression. *Ymeria* further demonstrates the high diversity of tetrapods in northeastern Greenland. Late Devonian.

Younginidae a late Permian family of small diapsid reptiles, generally considered lepidosauromorphs and now tentatively placed in the clade Neodiapsida. The type species *Youngina capensis* lived in Southern Africa at the end of the Permian and may have survived into the Triassic. Africa and Madagascar, late Permian.

Yuknessia a genus of colonial hemichordate animals in the class Pterobranchia. It extended long branches from a holdfast and is known from the Burgess Shale and two coeval sites. North America and Asia, middle Cambrian.

Yunnanocopia see **Lophogastrida**.

Yunnanolepis a genus of primitive placoderms in the order Antiarchi and family Yunnanolepididae. China and Vietnam, Early to Middle Devonian.

Yunnanozoon a genus of early hemichordate animals in the Chengjiang biota. *Yunnanozoon lividum*, similar to *Pikaia* of the Burgess Shale, may be the earliest-known hemichordate. China, early Cambrian, ca. 518 Ma.

Yutyrannus huali a species of large coelurosaurian dinosaurs in the superfamily Tyrannosauroidea. About 30 feet long and weighing 1.5 tons, *Yutyrannus* is the largest-known feathered dinosaur. The three specimens are also notable for being almost completely articulated fossils with three-fingered manus. Feathers are clearly present in several areas of the body, the longest being 8 inch neck feathers and 6 inch tail feathers. Yixian Formation, China; Early Cretaceous, 125 Ma.

Z

Zalambdalestidae a family of small, primitive eutherian mammals, now considered stem-eutherians and probably not placental. The shrew-like, mostly insectivorous *Zalambdalestes* was about a foot long. Mongolia, Late Cretaceous, possibly to Paleocene.

Zhelestidae a group of early mammals, poorly known although widespread. They have some ungulate traits and ranged in size from mouse to small ungulate. Known mainly from teeth and jaw fragments from the Late Cretaceous, they may have appeared as early as the Late Jurassic. Asia, Madagascar, Europe, and North America; Late Jurassic? To Late Cretaceous.

Zhongjianichthys a poorly known genus of basal chordate animals, possibly related to *Myllokunmingia*. Eel-like and jawless, it is about an inch long and has a thick skin and a ventral fin the length of its body. Chengjiang biota, China, early Cambrian, 518 Ma.

Zigzagiceras a genus of ammonoids in the order Ammonitida and family Perisphinctidae; Saudi Arabia, Middle Jurassic, 167–164 Ma.

Zoarium a collection of individual zooids that make up a compound or colonial organism. Some bryozoans form zoaria more than a foot wide.

Zone fossil see **index fossil.**

Zooecia singular zooecium, the chambers constructed by individual bryozoans.

Zooid an individual body unit of a colonial animal, especially graptoloids and bryozoans.

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Zosterophyllum a genus of primitive vascular land plants referred to as zosterophylls, in the paraphyletic class Zosterophyllopsida. One of the first vascular plants, it is distinguished by kidney-shaped sporangia growing near the ends of the branches. Global distribution, Silurian to Late Devonian.

Zuniceratops christopheri a genus of ornithischian dinosaurs in the suborder Ceratopsia. It is known from one skull and the bones of several individuals, found in New Mexico in 1996. Only 10 feet long and weighing less than 300 pounds, *Zuniceratops* seems to represent a transitional stage between the earliest ceratopsians and the larger, more familiar ones that were common in North America toward the end of the Cretaceous. United States, 91 Ma.

Zygentoma the silverfish, an extant order of insects previously grouped with the Archaeognatha in the obsolete order Thysanura. The Zygentoma are characterized by an elongate body, at least two cerci, and one medial extension on the tail. Cosmopolitan, known definitively from the Middle Devonian but probably originating in the late Silurian.

Zygolophodon a genus of mastodons, proboscideans in the family Mammutidae. One of the largest terrestrial mammals, it was 14 feet high at the shoulder, weighed 15–18 tons, and bore a pair of forward-projecting 13-foot tusks. Europe, Asia, Africa, and United States; Miocene to Pleistocene.

Zygoptera a suborder of flying insects in the order Odonata. They have a long and slender body, large compound eyes, and two pairs of wings. Compared to dragonflies, they are smaller (with a wingspan up to 7 inches), slightly built, weaker fliers, and generally fold their wings over the body. Female Zygoptera are generally larger than males. Global distribution, early Permian to Recent.

Zygospira a genus of small atrypid brachiopods in the family Anazygidae. It was biconvex and only half an inch wide, with strong ribbing. Global distribution Middle Ordovician to early Silurian.

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